Examining potential multi-scale drivers of flower visitor communities and plant-pollinator interactions in the context of tallgrass prairie habitat reconstruction

BY

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Dissertation Abstract

The processes governing community assembly, whereby species from a regional species pool colonize local sites, occur over a wide range of spatial and temporal scales. Studies of community assembly are fundamental to the fields of ecology and conservation, as developing our understanding of the drivers of species distributions and abundances will help advance ecological theory and will aid in the conservation and restoration of Earth's biodiversity. Insect pollinators are ideal systems for studies of community assembly, as they have been shown to be influenced both by fine-scale factors (e.g. the local provisioning of floral resources) and by the broader landscape context (e.g. the extent of natural lands surrounding focal sites). Moreover, our need to understand the drivers of pollinator community structure continues to increase, as pollinators worldwide have been shown to be declining due to numerous human-induced threats. In this dissertation, I evaluated multiple drivers of insect flower visitor community structure and plant-pollinator network architecture in the context of habitat reconstruction in the tallgrass prairie.

In Chapter 1, I assessed the effects of tallgrass prairie reconstruction on the structure of both forb and flower visiting insect communities. I found substantial differences in forb communities between these two types of prairie, but these differences largely did not extend to flower visitor communities, which were similar across remnant and reconstructed prairies. In Chapter 2, I assessed the extent to which flower visitor community structure was influenced by site-scale forb richness, abundance and composition, as well as the composition and configuration of the landscapes within which these sites were situated. My results indicate that flower visitors are largely not associated with site-scale forb α-diversity but may be strongly structured both by site-scale forb composition and landscape context. In Chapter 3, I used a

network approach to assess the efficacy of prairie reconstruction on plant-pollinator interactions. Plant-pollinator networks allow researchers to visualize community-wide interactions between forbs and flower visitors, and their structural properties can shed insight on the status and stability of plant-pollinator interactions at a given site. I found that network structure was very similar across remnant and reconstructed prairies, and that the particular features of these networks (i.e. modularity, robustness to species loss) suggest that plant-pollinator interactions have been reinstated. Taken together, my results suggest that habitat reconstruction has successfully re-established functioning communities of flower visitors in this system. In addition, my work indicates that landscape context likely plays a central role in structuring flower visitor communities in the highly modified and fragmented tallgrass prairie ecosystem.

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General Introduction

Understanding the processes that govern species co-occurrence at local scales has long been a fundamental goal in the field of ecology. Indeed, studies of community assembly—the process by which species from a regional pool colonize sites to form local communities (HilleRisLambers et al. 2012)—can be traced back to ecology's foundations as a science (e.g. Cowles 1899, Gleason 1927, Clements 1936). As the study of community assembly expands to include insights from a diverse array of fields, including biogeography, genetics, and ecosystems ecology, it is becoming increasingly apparent that the processes governing community assembly operate over a wide range of spatial and temporal scales (HilleRisLambers et al. 2012). Communities may be structured by local processes, including fine-scale abiotic conditions, resource competition, and feedbacks with soil microbiota (Whittaker 1952, Tilman 1980, Mangan et al. 2010). However, community assembly is also mediated by processes that take place on landscape and regional scales. For example, both theory and empirical evidence support a positive relationship between local species richness and regional species pool diversity (Ricklefs 2000, Hubbell 2001, Rahbek et al. 2007). In addition, the composition and configuration of habitat patches within a landscape can influence patterns of dispersal and can play a strong role in structuring local communities (Holzschuh et al. 2010, Myers et al. 2013, Senapathi et al. 2017). In recent years, there has been an increasingly strong call for ecologists to more fully explore how local-scale species distributions and interactions are modified by landscape- and regional-scale processes (Hubbell 2001, Leibold et al. 2004, Agrawal et al. 2007).

Pollinator communities are ideal systems within which to explore the interplay between local and landscape-scale processes. Pollinators require foraging resources (pollen, nectar), nest sites, and nesting materials (e.g. pithy stems, plant fibers) to complete their life cycles (Menz et

al. 2011). Many pollinators are highly mobile, and they search for and utilize these resources throughout the landscape (Roulston and Goodell 2010). Therefore, studies that address the drivers of pollinator community structure at focal sites, such as habitat restorations, must consider both the site-scale provisioning of resources, and the landscapes within which focal sites are situated (Kremen et al. 2007).

One further advantage to using pollinators to study community assembly stems from the recent adoption of network approaches to study plant-pollinator interactions. Plant-pollinator networks describe the community-wide interactions between forbs and animal pollinators (see Figures S3.1-S3.10 in Appendix 3 for examples). Network nodes are generally comprised of forb and pollinator species observed at a focal site, and links are typically based on visual observations of animals' visitation to flowers. This network approach has reinvigorated the field of pollination biology and has led to numerous advances in our understanding of pollinator ecology, evolution and conservation (Bascompte and Jordano 2007). For example, despite differing greatly in species composition, plant-pollinator networks worldwide have been shown to exhibit a shared suite of structural properties (see below), which suggests that there are likely common ecological mechanisms underpinning network buildup and stability (Bascompte and Jordano 2007). For studies of community assembly, a network approach allows researchers to expand beyond community descriptors such as species diversity and abundance to evaluate the processes that govern the assembly of the mutualistic interactions that ultimately shape the structural properties of plant-pollinator networks.

Studies of community assembly are becoming ever more critical as human activities put increasing pressure on Earth's biodiversity. Unfortunately, pollinators face a complex and interacting suite of human-induced threats, including global climate change, habitat degradation

and loss, and mortality from pesticides, parasites and disease (reviewed by Potts et al. 2010). This is incredibly concerning, as pollinators are critical to the maintenance of flowering plant diversity (almost 90% of extant angiosperms are animal-pollinated; Ollerton et al. 2011) and are integral to global food security (approximately 35% of global food crop production is pollinator-dependent; Klein et al. 2007). Anthropogenic threats have been linked to declines in pollinator populations and alterations in the composition of pollinator communities throughout the world (Biesmeijer et al. 2006, Bartomeus et al. 2013, Koh et al. 2016).

Habitat loss resulting from land use change is one of the primary threats to pollinator biodiversity (Potts et al. 2010). As such, studies addressing the multi-scale drivers of pollinator community structure in the context of habitat restoration have the potential to both further our understanding of community assembly and to yield valuable insights that can be used to further conserve and reinstate pollinator communities. Habitat loss has been particularly severe in North America's tallgrass prairie, where this dissertation research was conducted. Historically, the tallgrass prairie ecosystem encompassed well over 100 million ha throughout the United States and Canada (Samson and Knopf 1994). Agricultural conversion that accompanied Euro-American settlement has decimated this ecosystem; in some U.S. states, less than 1% of the historic extent of tallgrass prairie remains (Samson and Knopf 1994, Samson et al. 2004). In the face of these losses, a number of individuals and groups have sought to "restore" degraded, but never-plowed prairies as well as to "reconstruct" prairies *de novo* on former agricultural lands (terminology from Kurtz 2013).

Ecological restoration in general, as well as prairie restoration/reconstruction practices, have traditionally been botanically focused, emphasizing the restoration of the dominant vegetation that characterizes an ecosystem (Young 2000, Anderson 2009). However, the science

of restoration ecology has experienced dramatic growth in recent years, and the focus of ecological restoration has expanded to incorporate the restoration of a wider array of organisms (e.g. invertebrates, soil microbes) as well as the restoration of ecosystem functions such as nutrient cycling and pollination (Ruiz-Jaen and Aide 2005, Young et al. 2005, Montoya et al. 2012). Nevertheless, despite the critical importance of pollinators to ecosystems throughout the world, our understanding of the effects of ecological restoration on pollinator communities remains underdeveloped (Grass et al. 2016, Steiner et al. 2016, Kaiser-Bunbury et al. 2017). This is especially concerning in light of the aforementioned, widespread threats to pollinator populations.

As such, the overarching goal of this dissertation was to evaluate potential drivers of pollinator community structure and plant-pollinator interactions in the context of tallgrass prairie reconstruction. I addressed this overarching goal by assessing whether forb and insect pollinator (hereafter referred to as flower visitor) abundance, diversity and species composition differed between remnant (never plowed) prairies and prairies reconstructed on former crop fields (Chapter 1); by investigating the potential roles of site-scale forb communities and landscape composition and configuration on flower visitor community structure (Chapter 2); and by evaluating whether the architecture of plant-pollinator interaction networks, as well as networks' robustness to simulated species loss, differed between remnant and reconstructed prairies (Chapter 3). In the paragraphs below, I summarize the primary objectives and results of each chapter:

Chapter 1: Flower visitor communities are similar on remnant and reconstructed tallgrass prairies despite forb community differences.

Grasslands are one of the world's most extensive terrestrial ecosystems, and their agricultural value has made grasslands critical to global food security (O'Mara 2012). Unfortunately, grasslands worldwide have been subject to extensive anthropogenic habitat degradation (O'Mara 2012). As noted above, North America's tallgrass prairie has experienced extensive losses in total area due primarily to agricultural conversion that accompanied Euro-American settlement (Samson and Knopf 1994). Many remaining remnant (unplowed) prairies are small and isolated from other such remnants (Davis et al. 2008). Fortunately, interest in both prairie restoration and prairie reconstruction has grown over the past three decades (Anderson 2009).

Despite the increased attention paid to prairie restoration and reconstruction, reinstating prairie plant biodiversity remains challenging for several biological and logistical reasons. Forb-diverse seed mixes are often prohibitively expensive for practitioners, and many prairie forbs are not widely commercially available (Diboll 1997, Steinauer et al. 2003). In addition, legacy effects of previous vegetation and management on post-agricultural fields can influence the trajectory of restoration efforts (Kettle et al. 2000, Fuhlendorf et al. 2002, Foster et al. 2003, Rook et al. 2011). Competition with dominant C4 grasses and disruptions in the soil mycorrhizal community resulting from previous cultivation can also suppress forb diversity during prairie reconstruction (Weber 1999, Bever and Schultz 2003, Dickson and Busby 2009).

Historically, the focus of ecological restoration of tallgrass prairies has been on the difficult task of reinstating prairie plant communities (Anderson 2009). However, recent decades have seen both increasing attention paid to the restoration of ecosystem services (Devoto et al. 2012) and a rapid expansion of the field of pollination biology (Ollerton 2017). Because most prairie plants require animal-mediated (primarily insect) pollination for sexual reproduction

(Reed 1993), it is critical that we develop our understanding of the efficacy of prairie reconstruction in reinstating insect pollinator communities.

As such, I surveyed forbs and flower visiting insects across five remnant tallgrass prairies and five prairies reconstructed on former crop fields in northeast Kansas. Surveys were conducted from 2013-2015 and yielded a highly taxonomically resolved dataset comprising almost 7000 records of 326 insect taxa visiting 127 forb taxa. I compared the abundance, diversity and species composition of forbs and flower visiting insects (including the entire flower visitor community and two subgroups of flower visitors – bees and phytophagous beetles) between remnant and reconstructed prairies.

Given the known challenges of reinstating forb biodiversity during prairie reconstruction, I predicted that (1) prairie remnants would have higher forb diversity and abundance than reconstructed prairies, and that (2) remnant and reconstructed prairies would differ in forb species composition. I further predicted that (3) the flower visitor community (including both the bee and phytophagous beetle subgroups) would mirror that of the forb communities, exhibiting lower abundance and diversity on reconstructed prairies, as well as significant differences in species composition.

As expected, remnant and reconstructed prairies differed substantially in forb community structure—remnant prairies were significantly more forb-diverse, and forb composition differed significantly between the two types of prairie. Contrary to expectations, forb abundance was higher on reconstructed prairies, but only in the 2013 study year. Despite differences in the forb communities, the flower visitor community, including both subgroups, did not differ in diversity or abundance between remnant and reconstructed prairies. Only the bee community exhibited compositional differences; bee species composition was more variable on reconstructed, versus

remnant, prairies. Taken together, these results provide evidence that tallgrass prairie habitat reconstruction can be a valuable tool for re-establishing flower visiting insect communities. This work is published in *Restoration Ecology* 26(4): 751-759.

Chapter 2: Taxon-specific associations of tallgrass prairie flower visitors with site-scale forb communities and landscape composition and configuration

Many ecosystem services are provided by mobile organisms that utilize resources across spatial scales encompassing both the "focal" sites, where the provisioning of these services is measured, as well as the surrounding landscapes (Kremen et al. 2007). Pollination is one such service, with insect pollinators foraging for floral resources (pollen, nectar) and utilizing nest sites and nesting materials (e.g. plant fibers, mud, sand) among habitats that are often spatially segregated and embedded within anthropogenically modified landscapes.

Pollinators have been shown to respond positively to increasing floral resources at the scale of focal sites (e.g. crop fields, habitat restoration) (Steffan-Dewenter and Tscharntke 2001, Potts et al. 2003, Kennedy et al. 2013). Forb species composition may also structure pollinator communities at focal sites, as trophic specialization is common among many pollinator taxa (Robertson 1929, Ehrlich and Raven 1964).

In addition, pollinators are often influenced by the composition of the landscapes surrounding focal sites, typically exhibiting positive associations with the extent of surrounding natural/semi-natural lands and negative associations with surrounding agricultural lands (Kennedy et al. 2013, Senapathi et al. 2017). Pollinators' responses to landscape configuration (the spatial arrangement of habitats within a landscape) are less straightforward (Hass et al. 2018). Habitats within anthropogenically modified landscapes are often fragmented, making it

more likely for pollinators to encounter habitat edges (Fahrig 2003). Habitat edges have been shown to be both beneficial (e.g. Svensson et al. 2000) and detrimental (e.g. Ries and Debinski 2001) to pollinators. Even within the same landscape, pollinators' responses to habitat edges can be taxon specific (Ries and Debinski 2001, Holzchuh et al. 2010). Therefore, to more fully understand the drivers of pollinator community structure at focal sites such as habitat restorations, researchers must consider both the provisioning of floral resources at these sites as well as the composition and configuration of the landscapes within which these sites are situated (Kremen et al. 2007). Unfortunately, our understanding of the complex, multi-scale drivers of pollinator community structure remains underdeveloped (Grass et al. 2016, Senapathi et al. 2017).

To address this, I used the study system described in Chapter 1 to evaluate associations between tallgrass prairie flower visitors (the entire flower visitor community and three focal subgroups—bees, butterflies and syrphid/bombyliid flies) and (A) site scale forb α-diversity and species composition, and (B) the composition and configuration of the surrounding landscapes at two spatial scales—250 m and 1 km surrounding the sites. I predicted that α-diversity of flower visitors would be strongly associated with site-scale forb α-diversity, and that sites more similar in forb composition would also be more similar in flower visitor composition. I further predicted that flower visitor α-diversity would be positively associated with surrounding natural/semi-natural lands, and that associations involving landscape configuration (in this case, the extent of habitat edges) were likely to be largely negative, but could be taxon-specific.

I found that the composition of the forb community across the study sites was significantly associated with that of the flower visitor community as a whole. However, only bees were significantly, positively associated with site scale forb α-diversity. Relationships

involving landscape composition and configuration were more numerous and were taxon-specific. Butterfly richness was positively correlated with the combined extent of surrounding warm-season grasslands and woodlands, whereas bee and fly diversity were only associated with warm-season grasslands. In addition, bee and fly diversity were both higher in landscapes with more warm-season grassland edges, suggesting that habitat heterogeneity may be especially important for these groups. Taken together, this work indicates that landscape composition and configuration may be playing a stronger role in structuring flower visitor communities in this system than the site-scale provisioning of floral resources, but that these associations are taxon-specific. This work is in-press at *Biological Conservation*.

Chapter 3: Plant-pollinator networks exhibit similar structural properties and robustness to simulated species loss on remnant and reconstructed tallgrass prairies

Biotic interactions, including interactions between plants and their pollinators, are a fundamental component of ecosystems (McCann 2007). In recent years, researchers have increasingly begun to adopt a network approach to study mutualistic interactions, including plant-pollinator interactions. Plant-pollinator networks typically share a common suite of architectural features, and are often (A) highly nested, with specialist species interacting with proper subsets of the species that generalists interact with; (B) modular, consisting of compartments (modules) of species that frequently interact among themselves, but less frequently interact with members of other modules; and (C) characterized by connectivity distributions in which most species have few interaction partners and a small number of species have many interaction partners (Bascompte et al. 2003, Jordano et al. 2003, Olesen et al. 2007).

Assessments of the structural properties of plant-pollinator networks can generate important information about the structure and functioning of biological communities (Schleuning et al. 2015), which is likely to be especially relevant in light of the numerous human-mediated threats that pollinator communities face. Nevertheless, few studies have assessed the extent to which ecological restoration affects plant-pollinator network architecture (Kaiser-Bunbury et al. 2017).

In this chapter, I used the dataset described in Chapter 1 to generate a single plant-pollinator network for each of the ten tallgrass prairie sites in this study system. These networks consisted of all recorded interactions between forbs and their insect flower visitors from 2013 to 2015. Although the number of descriptors of network structure continues to increase, I focused this study's analyses on a set of six network properties that are particularly relevant in the contexts of ecological degradation and restoration (Memmott et al. 2004, Forup et al. 2008, Tylianakis et al. 2010, Nielsen and Totland 2014, Kaiser-Bunbury and Blüthgen 2015, Ribeiro da Silva et al. 2015, Soares et al. 2017): network size, network-level specialization (H_2'; Blüthgen et al. 2006), nestedness, modularity, networks' robustness to the simulated removal of flower visitor species, and the species-level interaction specialization (d'; Blüthgen et al. 2006) of plant and animal taxa shared among remnant and reconstructed prairies. I predicted that if prairie reconstruction efforts were successful in this system, network properties and robustness to simulated species removal would be similar across remnant and reconstructed prairies. Alternatively, if these efforts were unsuccessful, I predicted that plant-pollinator networks on reconstructed prairies would be smaller, and therefore less nested and less modular than those of remnant prairies, as the latter two properties are often associated with larger networks (Olesen et al. 2007, Moriera et al. 2015). I predicted that smaller, less nested and less modular networks

would, in turn, be less robust to simulated species removal, as both nestedness and modularity are believed to increase network stability (Krause et al. 2003, Memmott et al. 2004). Ecological restoration has been linked to increasing network complexity, and thus, higher network-level specialization. Therefore, I predicted that unsuccessfully reconstructed prairies in this system could be less specialized than reference, remnant sites. Finally, I predicted that systematic differences in species-level interaction specialization between remnant and reconstructed prairies could be indicative of both a lack of restoration success and fundamental differences in the structure and/or functioning of forb and flower visitor communities across these sites.

I found that network structural properties were very similar between remnant and reconstructed prairies. All networks, regardless of site type, were significantly non-nested, modular and specialized, which suggests that the partitioning of interactions (as opposed to interaction redundancy) is a key feature of these networks. Shared forb and flower visitor species also exhibited similar interaction specialization across remnant and reconstructed prairies. Moreover, all networks were highly robust in the face of simulated species loss. Taken together, these results provide compelling evidence that plant-pollinator interactions have been successfully reinstated across the reconstructed tallgrass prairies in this system.

Chapter 1: Flower visitor communities are similar on remnant and reconstructed tallgrass prairies despite forb community differences

Abstract

One common goal of habitat restoration and reconstruction is to reinstate the biodiversity found at intact, reference sites. However, few researchers have examined whether these practices reinstate communities of flower visiting insects. This is unfortunate, as anthropogenically-mediated declines in flower visitors, including bees (the primary pollinators in most terrestrial ecosystems), beetles, flies, and butterflies, have been reported worldwide. Biodiversity declines may be especially severe in North America's tallgrass prairie, a once-vast grassland that has experienced severe destruction and degradation due to agricultural conversion. As such, we assessed the structure of forb- and flower visiting insect communities as a whole, as well as two subsets of the flower visitor community—bees and phytophagous beetles—across five tallgrass prairie remnants and five reconstructed prairies (former crop fields) in Kansas from 2013-2015. Remnant prairies had significantly higher forb diversity and differed significantly in forb composition, compared to reconstructed prairies. Despite the dissimilarities in forb community structure, there were no differences in flower visitor diversity or abundance between remnants and reconstructed prairies. However, when considered separately, bee communities exhibited significantly greater variability in composition on reconstructed prairies, likely due to the abundance of generalist bee species visiting non-native legumes at two reconstructed prairies. Our work provides evidence that prairie habitat reconstruction is a valuable tool for re-establishing flower visiting insect communities and also emphasizes the considerable role that non-native species may play in structuring grassland plant-bee interactions.

Introduction

Interactions between plants and flower visiting insects have wide ranging ecological and economic impacts. For example, almost 90% of flowering plants rely on animal-mediated pollination for sexual reproduction, and 35% of global crop production depends on pollinators (Klein et al. 2007; Ollerton et al. 2011). Insects comprise the majority of pollinators (Grimaldi & Engel 2005), and bees are the most important pollinators for most terrestrial ecosystems and major plant families (Greenleaf 2007; Cane 2008). Phytophagous insects also have multiple, complex effects on plant communities. Insect herbivores can reduce primary productivity, promote carbon- and nutrient cycling, and alter plant community structure (Whiles & Charlton 2006; Allan & Crawley 2011; Metcalfe et al. 2014).

Unfortunately, flower visiting insects throughout the world face numerous anthropogenic threats (Biesmeijer et al. 2006; Koh et al. 2016). Foremost among these threats is habitat loss that often accompanies agricultural intensification (Potts et al. 2010). Grasslands are one of the most extensive terrestrial ecosystems and play a critical role in global food security, yet grasslands worldwide have been subjected to extensive human-mediated degradation (O'Mara 2012). Tallgrass prairie in different U.S. states has experienced declines in area ranging from approximately 82-99%, primarily due to agricultural conversion that accompanied Euro-American settlement (Samson & Knopf 1994). Despite these losses, remnant (native, unplowed) prairies remain, ranging from large, contiguous tracts (*e.g.* the Flint Hills of eastern Kansas) to small, isolated prairie hayfields and roadside strips (Davis et al. 2008). In addition, individuals and groups have rehabilitated degraded, but never-plowed prairies (herein referred to as restored prairies) and have re-established prairies on former croplands (herein referred to as reconstructed prairies; Kurtz 2013). This is typically accomplished by planting native grasses and forbs and by

reinstating historic disturbance regimes (e.g. fire, grazing) that are key to reinstating prairie forb biodiversity (Kurtz 2013). Although empirical assessments of restoration success have increased in recent years (Wortley et al. 2013), the extent to which the reconstruction or restoration of plant communities can reinstate communities of flower visitors remains understudied (Grass et al. 2016; Steiner et al. 2016; Kaiser-Bunbury et al. 2017).

The colonization success of flower visitors likely varies widely among restored and reconstructed lands for several reasons (Harmon-Threatt & Hendrix 2015). Highly anthropogenically modified landscapes can limit the extent to which some flower visitors are able to disperse to focal sites (Dixon 2009; Menz et al. 2011). Site-scale forb diversity and abundance have also been shown to affect flower visitor diversity and abundance (Potts et al. 2003; Hines & Hendrix 2005; Kwaiser & Hendrix 2008; but see Davis et al. 2008; Grass et al. 2016). Reconstructed prairies often have lower plant diversity than remnant prairies, and they may differ from remnants in plant community composition (Kindscher & Tieszen 1998; Sluis 2002; Middleton et al. 2010; Carter & Blair 2012). Multiple factors, including financial constraints, seed availability, and restoration goals can impact the richness and composition of prairie seed mixes (Harmon-Threatt & Hendrix 2015), suggesting that native forb communities may also differ substantially among reconstructed prairies.

Furthermore, reconstructed prairies often face intense invasive propagule pressure resulting from long periods of agricultural production, and low diversity reconstructed prairies may be more susceptible to invasive plant species (Yurkonis 2013). Invasive plants can alter plant composition and diversity by suppressing native species (Christian & Wilson 1999; Reed et al. 2005; Goldblum et al. 2013), and they can have complex, and often highly variable, effects on flower visiting insects (Larson et al. 2006; Stout & Morales 2009). Non-native and invasive

plants can alter visitation patterns of flower visiting insects and can attract different suites of flower visitors than native plant communities (Morales & Aizen 2006), including a greater degree of generalists (Memmott & Waser 2002; Larson et al. 2006).

The goal of this study was to assess the extent to which the reconstruction of prairies on former croplands can reinstate the diversity, abundance and composition of forbs and flower visiting insects found on remnant sites. We predicted that: **I)** Prairie remnants would have higher forb diversity and abundance than reconstructed prairies; **II)** Reconstructed prairies would differ significantly in forb composition, and would be more variable in composition than remnants. Mirroring the predicted differences in forb communities, we further predicted that **III)** flower visitor communities as a whole, as well as bees (the primary pollinators in tallgrass prairies (Harmon-Threatt &Hendrix 2015)) and phytophagous beetles considered independently, would exhibit lower diversity and abundance on reconstructed prairies; **IV)** flower visitor, bee, and phytophagous beetle communities would differ in composition on remnants and reconstructed prairies and would be more variable on reconstructed prairies.

Methods

Study Sites

The study was conducted in the tallgrass prairie-deciduous forest ecotone of northeast Kansas. From 2013-2015, we surveyed forbs and flower visiting insects at five remnant tallgrass prairies (AND, GUE, ROC, SNY, TEA) and five reconstructed prairies (BAK, BUS, BYE, COO, KET; Fig. 1.1; Table S1.1 in Appendix 1). Reconstructed prairies were (mean $\pm$ 1SE) 4.78 $\pm$ 0.69 ha and remnants were 4.64 $\pm$ 0.48 ha (range for all sites: 3.1-7.0 ha). Sites greater than 5-km away from one another were chosen to minimize the possibility that flower visiting insects could travel among sites. The reconstructed prairies were seeded with native forbs and grasses by

the landowners and ranged in age from 4-21 years (Table S1.1). All sites except BYE were burned or hayed at least once between 2013-2015.

Sampling Methods

In spring 2013, we established a 100 x 100 m study plot near the center of each site, which remained in place for all survey years. Surveys were conducted near midday (10AM-3PM) on days when temperatures were greater than 16°C with no precipitation and wind speeds less than approximately 15 km/h. Sites were sampled 2-4 times annually, depending on weather and the timing of management practices (Table S1.1). Each year, we commenced surveying in late-April to mid-May and stopped surveying in late July, when most of the sites were hayed or mowed. All surveys were conducted by the same investigator to maximize the consistency of the surveying techniques. Each of the 99 surveys was conducted using a three-step approach:

Transect Sampling: We established four 20 m transects running north-south within the study plot. Each 50 x 50 m quarter of the study plot contained one transect. Transect position within each quarter was determined by drawing a random number pair from a random number table. Transect positions were re-randomized for each survey. We walked the length of each transect twice, recording all insects that we observed in contact with the reproductive structures of open flowers, up to 1.3 m (the length of the insect net) away from the transect line, on both sides of the line (20 x 2.6 m = 52 m^2 total sampling area per transect). When feasible, we hand-netted insects and placed them individually into plastic vials, labelled with the forb species it was visiting. Visitor species of conservation concern were recorded, but individuals were not captured. For highly abundant visitor (morpho)species, we first collected several individuals for later identification, then tallied subsequent individuals we observed "on the wing". Because of logistical difficulties associated with detecting tiny insects, we only recorded flower visitors

greater than approximately 2 mm in length. Insects were freeze-killed, mounted in the laboratory, and identified (see Acknowledgements). A literature search was conducted to identify diet- and habitat specialists for two abundant groups of flower visitors, bees and butterflies, as well as to identify beetles that are phytophagous in their adult stage, in order to more fully characterize the flower visitor communities across the study sites. Voucher specimens are housed in the California State Collection of Arthropods (Diptera) and the Snow Entomological Collection at the University of Kansas (all other Orders).

Timed Sampling: Typically, not all currently-flowering forb species at a site were represented along the transects. Therefore, in order to more fully characterize forb- and flower visitor communities, we walked through the 100 x 100 m study plot for 60 additional minutes, opportunistically recording flower visitors. We spent approximately 15 minutes surveying each 50 x 50 m quarter of the plot.

Forb Sampling: Finally, we walked each transect again, recording the species identities and the size of the floral display of all flowering forbs within the same sampling area used for flower visitor surveys. We used a clear, plastic grid of 2 x 2 cm squares to estimate the floral display size for all flowering forbs within this area, and this measure was used for our estimates of forb abundance. For highly abundant forbs, it was not feasible to measure the total size of the floral display along the entire transect. For these forbs, we established either four 0.5 x 0.5 m- or four 1 x 1 m quadrats, depending on forb size and abundance, at 5 m intervals along the transect. We summed the total floral abundance across these quadrats, using the grid method outlined above, and multiplied this number by a conversion factor (52 for 0.5 x 0.5 m quadrats; 13 for 1 x 1 m quadrats) to estimate the total size of the floral display within the 52 m^2 sampling area.

Statistical Analyses

Diversity of the four focal groups—flowering forbs, all flower visitors, bees, and phytophagous beetles—was measured as the effective number of species ($e^{H'}$; Jost 2006). Sampling effort differed among sites (Table S1.1). Therefore, we first verified, via linear models, that diversity was not significantly affected by the total number of site visits ($P > 0.05$). As such, the "sampling effort" term was not included in the main analyses of diversity. We used linear mixed-effects models to assess differences in the diversity of each focal group due to site type (fixed effect: remnant, reconstructed prairie), year (fixed effect: 2013, 2014, 2015) and their interaction. To account for variation among sites, "site" was modelled as a random effect. Models were fit in R, version 3.3.2 (R Core Team 2016), using the package 'nlme' (Pinheiro et al. 2017).

We rarefied the 2013 and 2014 abundance values for each of the four focal groups to three samples per year, using the R package 'rich' (Rossi 2011) to account for differences in sampling effort. For the 2015 data, no rarefactions were performed, as nine of the 10 sites were sampled three times. We used generalized linear mixed-effects models (Poisson error distribution) using 'lme4' in R (Bates et al. 2015) to model the effects of site type, study year, and their interaction on the abundance of each focal group. "Site" was modelled as a random effect, and an observation-level random effect was added to account for overdispersion (Harrison 2014). Type III tests of fixed effects were performed using parametric bootstrapping in the R package 'afex' (Singmann et al. 2017). Treatment contrasts were implemented when necessary.

We conducted repeated-measures PERMANOVAs in PRIMER-E v6 (Clarke et al. 2006), using relative abundance data and Bray-Curtis dissimilarity, to assess differences in composition due to site type, study year and the site type x study year interaction for the four focal groups. Indicator Species Analysis (Dufrêne & Legendre 1997; R package 'indicspecies', De Cáceres &

Legendre 2009) was used, when necessary, to identify species significantly associated with a particular site type or study year. We categorized forbs indicative of each site type based on their Kansas Coefficient of Conservatism (CoC) values (Freeman 2012). CoC values range from 0-10; species with higher numbers are typically restricted to high quality habitats, while species with lower numbers are considered weedy or opportunistic.

We used PERMDISP (R package 'vegan', Oksanen et al. 2016) to assess whether each of the four focal groups exhibited significantly more compositional variability among reconstructed prairies, versus remnants. PERMDISP was used to examine multivariate dispersion due to site type, regardless of whether the PERMANOVAs revealed a significant effect of site type, to test the prediction that reconstructed prairies had significantly greater compositional variability. Upon finding a significant dispersion effect for bee communities, we used non-metric multidimensional scaling to visualize differences in dispersion between remnants and reconstructed prairies. For the "study year" term in the PERMANOVA models, PERMDISP was used as a post hoc test, to examine whether significant differences occurred due to location or dispersion effects (Anderson 2001). When necessary, we performed pairwise comparisons in PRIMER-E to assess compositional differences among study years.

Results

Field Surveys

We conducted 99 surveys from 2013-2015, yielding 6679 records of 326 insect taxa visiting 127 forb taxa. Eighty-five percent of insects were identified to species, with 97% resolved to genus, sub-genus or species level. Eighty-nine percent of forb taxa were identified to species, with 97% identified to genus or species level. Based on abundances of individuals, the flower visitor community consisted of 33% Coleopterans, 33% Hymenopterans, including 15

oligolectic (pollen-specialist) bee species and five cleptoparasitic (brood parasite) bee species, 15% Dipterans, 14% Lepidopterans (including nine likely prairie habitat specialist species), 4% Hemipterans, and less than 0.01% "other/unidentified" (Table S1.2). All beetles we recorded are considered phytophagous, except for predacious beetles in the family Coccinellidae (ladybird beetles) and the genus *Lebia* (Carabidae).

Forb Communities

Remnants and reconstructed prairies differed substantially in forb community structure. Forb abundance was significantly higher on reconstructed prairies in 2013 only (year: $\chi^2_{[2]} = 9.57$; $P = 0.011$; site type x year: $\chi^2_{[2]} = 9.71$; $P = 0.023$; Table S1.3; Fig. 1.2). Forbs were approximately 10 times more abundant on reconstructed prairies in 2013, versus remnants, largely due to two non-native forbs, *Melilotus officinalis* (yellow sweet clover) and *Trifolium campestre* (hop trefoil), which together comprised 66% of total forb abundance on reconstructed prairies. There was a marginal, though non-significant, effect of site type on forb abundance ($\chi^2_{[1]} = 4.68$; $P = 0.064$; Table S1.3), as abundance tended to be higher on reconstructed sites in all study years. Forb diversity was significantly higher on remnants ($F_{[1,8]} = 8.08$; $P = 0.022$; Table S1.4; Fig. 1.3) but exhibited neither significant interannual variation nor a significant site type x year interaction ($P > 0.05$).

Forb composition also differed significantly between remnant- and reconstructed prairies (*pseudo*-$F_{[1,8]} = 1.50$; $P = 0.014$; Fig. 1.4, Table S1.5). Six forb species were significant indicators of reconstructed prairies, and 17 species were indicators of remnants (Table S1.6). Most species indicative of reconstructed prairies were weedy or opportunistic species with low CoC values (e.g. *Rudbeckia hirta* (black-eyed susan)). Significant indicators of prairie remnants

included species such as *Phlox pilosa* (downy phlox) that are typically restricted to high-quality, intact prairies, as well as non-native species such as *Leucanthemum vulgare* (ox-eye daisy).

There was also significant interannual variation in forb composition between the 2014 and 2015 study years (PERMANOVA: *pseudo-*$F_{[2,16]}$ = 1.66; P = 0.031, Table S1.5; 2014 v. 2015 pairwise comparison: t = 1.586, P = 0.021), but not between any other pairs of study years (P > 0.05). Two species were significant indicators of the 2015 study year—*Erigeron strigosus* (daisy fleabane) (P = 0.024) and *Silphium laciniatum* (compass plant) (P = 0.006). No forb species were significantly associated with the 2014 study year at the α = 0.05 significance level. There was no significant site type x year interaction (P > 0.05; Table S1.5), and no compositional differences were attributable to differences in community level dispersion (PERMDISP: P > 0.05).

Flower Visitor Communities

Unlike the forb community, the flower visitor, bee and phytophagous beetle communities did not exhibit differences in diversity or abundance between remnant- and reconstructed prairies. For all flower visitors and for bees, there were no significant differences in diversity or abundance due to site type, study year, or the site type x study year interaction (P > 0.05; Table S1.7-S1.8). Similarly, phytophagous beetle diversity did not differ significantly due to site type, year or their interaction (Table S1.7). Phytophagous beetle abundance did not differ between remnants and reconstructed prairies, but beetles were significantly less abundant in 2015, compared to 2013 and 2014 (year: $\chi^2_{[2]}$ = 8.72; P = 0.026; Table S1.8; treatment contrasts: $P_{2013v2015}$ = 0.00751; $P_{2014v2015}$ < 0.0001).

Of all focal insect groups, only the bee community exhibited compositional differences between remnants and reconstructed prairies. Bee composition was marginally, though non-

significantly, affected by site type (PERMANOVA: pseudo-$F_{[1,8]}$ = 1.85; P = 0.061; Table S1.9), and bee communities were significantly more variable in composition on reconstructed prairies versus remnants (PERMDISP: pseudo-$F_{[1,8]}$ = 6.628; P = 0.039; Fig. 1.5). There were no significant compositional differences between remnants and reconstructed prairies for flower visitors as a whole, or phytophagous beetles (PERMANOVA: P > 0.05, Table S1.10-S1.11; PERMDISP: P > 0.05).

The two reconstructed prairies furthest from the group centroid for bee community composition were KET and BAK (Fig. 1.5). These sites were each strongly structured by a single, generalist bee species interacting with a non-native legume species. Thirty-seven percent of all forb-bee interactions recorded at KET between 2013-2015 involved the common, native generalist *Bombus bimaculatus* (two-spotted bumble bee) visiting *Trifolium pratense* (red clover). Six additional native bee species were also recorded on *T. pratense* at KET. At BAK, 62% of all forb-bee interactions consisted of *Apis mellifera* (European honeybee) visiting *M. officinalis*. *Melilotus officinalis* was also visited by 17 native bee species at BAK.

The species composition of the focal insect groups exhibited strong interannual variation. There was significant interannual variation the composition of flower visitors (PERMANOVA: *pseudo-*$F_{[2,16]}$ = 3.46; P = 0.001; Table S1.10), bees (PERMANOVA: *pseudo-*$F_{[2,16]}$ = 3.51; P = 0.002; Table S1.9), and beetles (PERMANOVA: *pseudo-*$F_{[2,16]}$ = 2.29; P = 0.032; Table S1.11). This was not due to differences in dispersion for any insect group (PERMDISP: P > 0.05). Flower visitor composition differed significantly among all three study years (2013 v. 2014: t = 1.534, P = 0.019*;* 2013 v. 2015: t = 1.940, P = 0.008*;* 2014 v. 2015: t = 2.063, P = 0.005). Seven flower visitor taxa were significant indicators of the 2013 field season, three taxa were significantly associated with 2014, and nine taxa were significantly associated with 2015 (Table

S1.12). Bee composition also significantly differed across all three study years (2013 v. 2014: t = 1.529, P = 0.047; 2013 v. 2015: t = 2.081, P = 0.007; 2014 v. 2015: t = 1.990, P = 0.006). Indicator Species Analysis of the bee community closely mirrored that of the flower visitor community (Table S1.12). Phytophagous beetle composition in 2013 was significantly different from both 2014 (t = 1.90, P = 0.031) and 2015 (t = 1.72; P = 0.044). The weevil *Odontocorynus salebrosus* was significantly associated with the 2013 study year (P = 0.031; Table S1.12). No other phytophagous beetle species was a significant indicator of any study year. No significant site type x year interactions were detected for any insect group (P > 0.05).

Discussion

Our findings indicate that prairie reconstruction is successfully reinstating several aspects of flower visitor communities. Despite differences among reconstructed prairies in age, management history, and forb community structure, we found that flower visitor diversity, abundance and composition on reconstructed prairies were similar to remnant prairies. However, bees, the primary pollinators for tallgrass prairies, were more variable in composition on reconstructed prairies. This was largely driven by bees' interactions with non-native legumes, highlighting the influence that non-native forbs can have on plant-bee interactions in the context of habitat reconstruction.

The observed differences in forb community structure between remnants and reconstructed prairies were unsurprising, as many factors can impede forb re-establishment in tallgrass prairies. Forb-diverse seed mixes are often expensive, and seeds of many prairie forbs are not widely commercially available (Diboll 1997, Steinauer et al. 2003). These constraints likely affected forb diversity at the reconstructed sites, as several prairie remnant indicator species were spring- or early-summer blooming species, which are often underrepresented in

prairie seed mixes (Carter & Blair 2012). The highly abundant non-native legumes *M. officinalis* and *T. campestre* recorded across several reconstructed prairies also contributed to the significant differences in forb abundance we observed in 2013. It is important to note that we recorded several non-native forb species during our surveys, many of which, including *T. campestre,* are not typically considered invasive in tallgrass prairies. However, *M. officinalis* can be invasive in grasslands (Gucker 2009) and thus may pose a threat to the re-establishment of prairie forb communities. Several other factors, including legacy effects of previous vegetation and management (Kettle et al. 2000; Fuhlendorf et al. 2002; Foster et al. 2003; Rook et al. 2011), competition with C4 grasses (Weber 1999; Dickson & Busby 2009), and alterations in the soil microorganism community resulting from cultivation (Bever et al. 2003) also likely contributed to the observed differences in forb communities.

Despite differences in the forb communities, our work suggests that flower visitors are successfully re-establishing on reconstructed prairies. This concurs with a small but growing body of literature demonstrating that the re-establishment of grassland flower visitors can accompany plant community restoration (Ries et al. 2001; Forup & Memmott 2005; Hopwood 2008; Tarrant et al. 2013). The reconstructed prairies in this study varied in sown species density and disturbance regimes, indicating that there are likely multiple suitable methods of reconstructing prairies to reinstate flower visitors. The reconstructed prairies also varied in age, suggesting that flower visitors respond relatively quickly to prairie reconstruction. This has recently been demonstrated for bee communities on reconstructed prairies in Illinois, USA (Griffin et al. 2017). However, it is unclear whether these findings are applicable to other ecosystems, as there are substantial geographical differences in the diversity and specialization of plant-pollinator interactions (Johnson & Steiner 2000). For example, in ecosystems

characterized by specialized plant-pollinator interactions (e.g. the Cape flora of South Africa) flower visitor re-establishment will likely prove more challenging (Menz et al. 2011). In addition, although flower visitor communities were similar on remnants and reconstructed prairies, the composition of all focal insect groups exhibited significant interannual variation, highlighting the need for practitioners monitoring flower visitors to sample across multiple years.

The only clear difference in flower visitor community structure that we observed between site types was the significantly greater compositional variability of bees on reconstructed prairies. This trend was mediated by *M. officinalis* and *T. pratense*, which were highly abundant at two reconstructed prairies and attracted large numbers of *A. mellifera* and *B. bimaculatus* workers. This result highlights the contrasting roles that non-native plants can have in habitat reconstructions. Both species may be targeted for removal by practitioners wishing to suppress non-native forbs. Nevertheless, native bees visit a wide variety of non-native, invasive plants (Stout & Morales 2009), and non-native plants such as *T. pratense*, which is not considered invasive in the Great Plains (Great Plains Flora Association 1986) may be provisioning key resources for native bees in highly human-modified landscapes (Westphal et al. 2003). Indeed, two species we observed visiting *T. pratense*, *Bombus pensylvanicus* (American bumble bee) and *Bombus fraternus* (southern plains bumble bee), are IUCN-listed as vulnerable and endangered, respectively (Hatfield et al. 2014; Hatfield et al. 2015). Therefore, practitioners should accompany any suppression of non-native forbs that native bees may be utilizing with the reintroduction of native species with similar flowering periods, to limit the interruption of foraging resources as much as possible.

We did not observe a similar trend for the other focal insect subgroup—phytophagous beetles. Neither *T. pratense* or *M. officinalis* was visited extensively by phytophagous beetles,

and most of the abundant phytophagous beetle species (*e.g. Diabrotica cristata*) typically visited a variety of forbs across numerous remnant and reconstructed prairies.

It is important to note that we did not sample non-reconstructed sites. Given our lack of data on flower visitors prior to prairie reconstruction, an alternative interpretation is that neither the remnants nor the reconstructed prairies are sustaining functioning pollinator communities. Our study sites are all fewer than 10 ha and are embedded in landscapes with varying degrees of intensively managed lands (K.R. Denning, unpublished data). It is possible that even forb-diverse remnants may be too small to provide sufficient resources for flower visitors if they are embedded in highly-modified landscapes. Resource-poor landscapes can also limit the extent to which flower visitors can access focal sites (Dixon 2009). However, we consider this alternative interpretation unlikely. Diet- and habitat specialists are especially susceptible to ecosystem degradation (Biesmeijer et al. 2006; Dixon 2009; Bates et al. 2011; Bartomeus et al. 2013). Therefore, we predict that sites with degraded flower visitor communities would be characterized by low abundance and diversity and few specialists. In contrast, we found that two abundant groups of flower visitors, bees and butterflies, were characterized by numerous oligolectic species and habitat-specialists, respectively. We also recorded five cleptoparasitic bee species, a life history trait hypothesized to be especially vulnerable to disturbance (Sheffield et al. 2013). Therefore, we consider it more likely that remnant and reconstructed prairies are functioning as relatively high quality "oases" for flower visitors in highly modified landscapes. Further work is necessary to assess the extent to which flower visitors are nesting/overwintering at these sites, as opposed to utilizing the sites for foraging only.

As the human population continues to rise, putting increasing pressure on Earth's remaining natural lands, the need for ecological restoration is becoming more critical. Our work

provides support for the role that habitat reconstruction can play in reinstating communities of flower visiting insects in tallgrass prairies, North America's most endangered ecosystem (Samson & Knopf 1994). Future work in this system will assess the extent to which land-use in the surrounding landscapes influences the structure of flower visitor communities at these sites, in addition to examining the structural properties of plant-flower visitor networks in the context of prairie reconstruction.

Figures and Tables

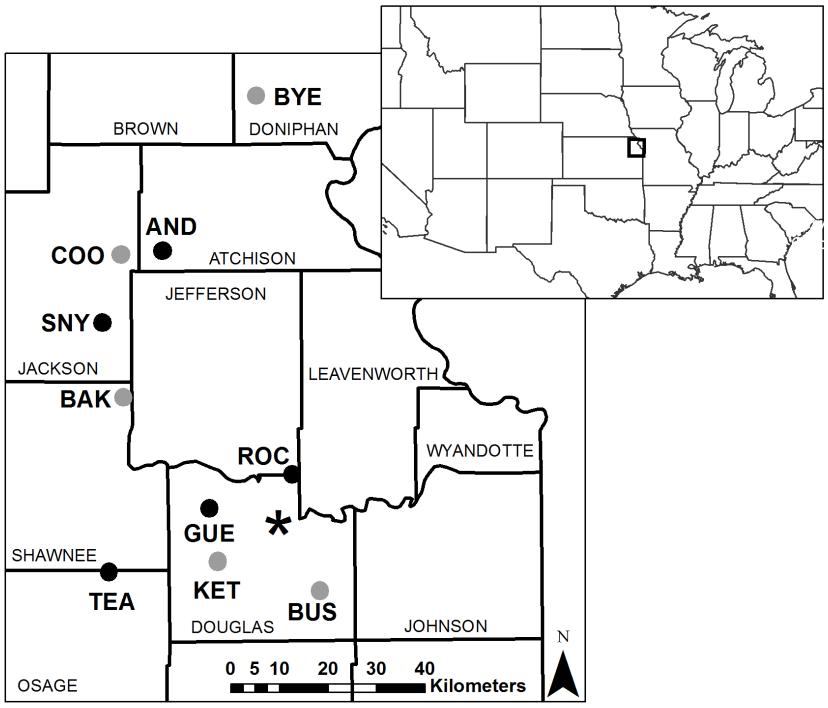

Figure 1.1. Map of study sites in northeast Kansas. Prairie remnant sites are labelled in black, and reconstructed sites are labelled in grey. Kansas counties are listed for reference. The asterisk denotes Lawrence, KS.

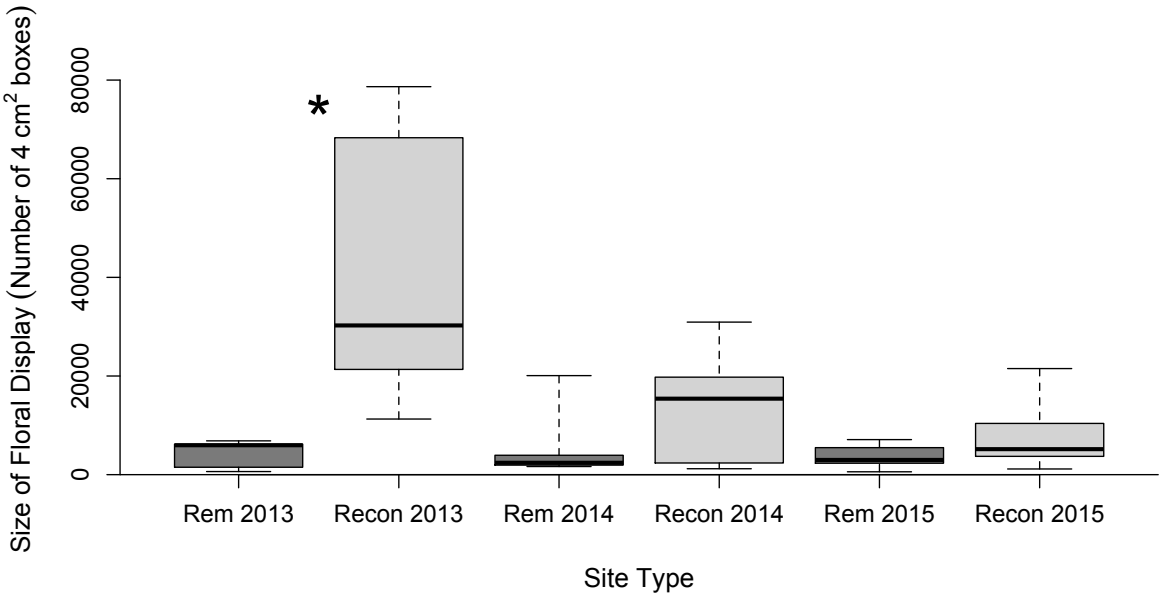

Figure 1.2. Forb abundance across remnant (rem) and reconstructed (recon) prairies in 2013, 2014, and 2015. The asterisk indicates a significant difference in abundance between site types in 2013 ($P_{2013} < 0.0001$) based on treatment contrasts after a significant site type x study year interaction from a generalized linear mixed model ($P = 0.023$).

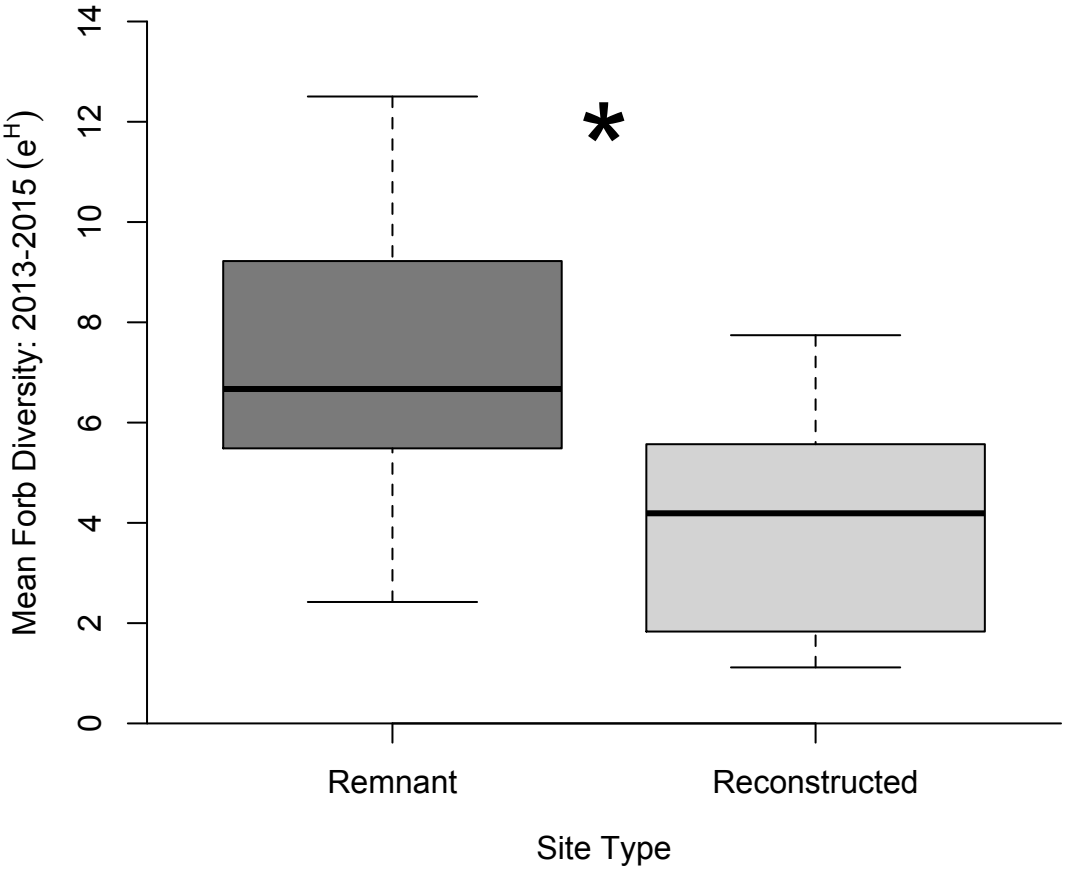

Figure 1.3. Mean forb diversity ($e^{H'}$) of prairie remnants and reconstructed prairies from 2013-2015. Boxplot whiskers represent extreme values for each site type, and box edges represent the first and third quartiles of the data. The asterisk indicates a significant difference in forb diversity based on a linear mixed model ($P = 0.022$).

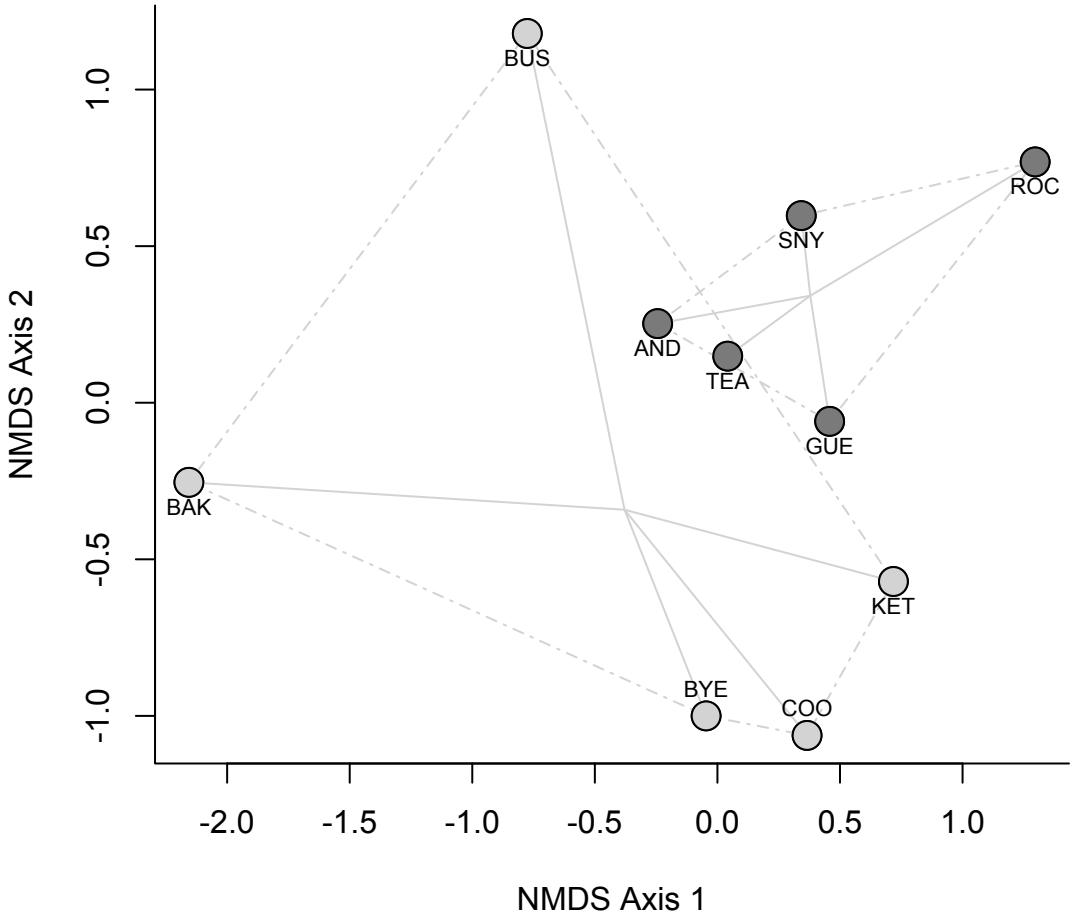

Figure 1.4. NMDS ordination of forb community composition across five prairie remnants (dark grey) and five reconstructed prairies (light grey) from 2013-2015.

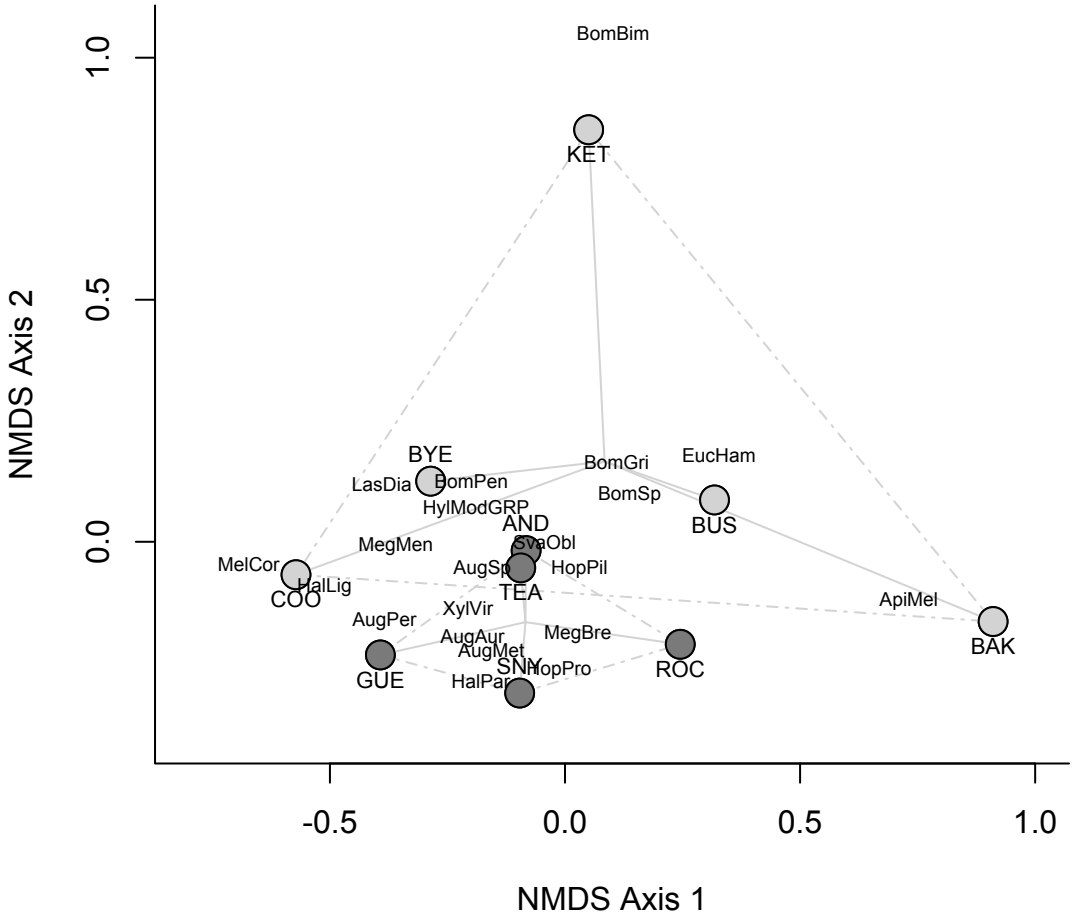

Figure 1.5. NMDS ordination of bee community composition across prairie remnants (dark grey) and reconstructed prairies (light grey) in northeast Kansas. Species scores for bee species with >10 total individuals recorded between 2013 and 2015 are displayed. Species displayed are: ***Api**s **mel**lifera, **Aug**ochlorella **aur**ata, **Aug**ochloropsis **met**allica, **Aug**ochlorella **per**similis, **Aug**ochlorella **sp**p., **Bom**bus **bim**aculatus, **Bom**bus **gri**seocollis, **Bom**bus **pen**sylvanicus, **Bom**bus **sp**p., **Euc**era **ham**ata, **Hal**ictus **lig**atus, **Hal**ictus **par**allelus, **Hop**litis **pil**osifrons, **Hop**litis **pro**duct, **Hyl**aeus **mod**estus morphospecies group (H. modestus, H. affinis, H. illinoisensis, H. undescribed sp. A), **Meg**achile **bre**vis, **Meg**achile **men**dica, **Mel**issodes **cor**eopsis, **Las**ioglossum (**Dia**lictus) spp., **Sva**stra **obl**iqua, **Xyl**ocopa **vir**ginica.*

Chapter 2: Taxon-specific associations of tallgrass prairie flower visitors with site-scale forb communities and landscape composition and configuration

Abstract

Pollinators are integral to global plant biodiversity and agroecosystems, yet our understanding of the multi-scale drivers of pollinator community structure remains underdeveloped. In this study, we used a dataset comprising almost 7000 highly taxonomically resolved records of tallgrass prairie forbs and flower visiting insects to evaluate potential roles of site-scale forb communities as well as the composition and configuration of the surrounding landscapes, in structuring flower visitor communities. We examined the whole flower visitor community and three focal subgroups—bees (the principal pollinators worldwide), butterflies (often less efficient pollinators, but potentially useful as indicator taxa) and syrphid/bombyliid flies (which, as non-bee taxa, are often overlooked). At the site-scale, the composition of the entire flower visitor community was significantly associated with forb composition, but only bees were significantly, positively associated with forb α-diversity. Bee, butterfly, and fly diversity exhibited taxon-specific relationships with landscape composition and configuration. Butterfly richness was positively correlated with the combined extent of warm-season grasslands and woodlands, whereas bees were associated with the extent of warm-season grasslands, only. Bee and fly diversity was higher in landscapes with greater grassland edge density, indicating that habitat heterogeneity may be beneficial for these taxa. Our work adds to the growing body of research indicating that pollinators' responses to floral resources and land use in highly modified landscapes are often complex, taxon-specific and scale dependent, and our results highlight the importance of distinguishing among different types of natural and semi-natural lands when formulating pollinator conservation and restoration plans.

Introduction

Pollinators are critical to the maintenance of plant biodiversity and agroecosystems worldwide. Almost 90% of flowering plants are animal-pollinated (Ollerton et al. 2011), and over one-third of global crop production is pollinator-dependent (Klein et al. 2007). Despite their importance, it is becoming increasingly apparent that multiple human-mediated pressures are threatening pollinator populations. Foremost among these threats is habitat loss (Brown and Paxton 2009) which often accompanies agricultural intensification (Bukovinszky et al. 2017).

Although bees are the world's primary pollinators (Cane 2008), a recent review by Ollerton (2017) has emphasized the incredible taxonomic diversity of insect pollinators. Unfortunately, monitoring and conserving insects, which comprise the majority of pollinators (Grimaldi and Engel 2005), remains challenging for several reasons. Insect communities are often species-diverse and exhibit a wide variety of life history traits, making it difficult to formulate comprehensive conservation plans that encompass their wide-ranging resource requirements (Shuey 2013). Furthermore, many insects (e.g. bees; Cane 2001) are difficult to identify without specialized training or the assistance of taxonomists. This underscores the need to evaluate the utility of more easily-identified insect groups (e.g. butterflies) as indicators for the responses of these taxa.

Conservation of insect pollinators is further complicated by their mobility, as pollinators often utilize resources across spatial scales that encompass both focal sites (e.g. crop fields, habitat restorations) and the surrounding landscapes (Kremen et al. 2007). Pollinators often respond positively to increasing site-scale floral resources (Steffan-Dewenter and Tscharntke 2001, Potts et al. 2003, Marini et al. 2009, Kennedy et al. 2013), but researchers in many systems have also found that relationships between forb- and pollinator α-diversity are weak or absent

(e.g. Davis et al. 2008, Grass et al. 2016). Plant species composition at a focal site may also play an important role in structuring pollinator communities, as many pollinators exhibit strong trophic specialization as larvae and/or adults (Robertson 1929, Ehrlich and Raven 1964, Kopper et al. 2000) and will be unable to successfully colonize a site unless specific plants are present.

In addition to responding to site-scale floral resources, pollinators often exhibit strong associations with the composition of the surrounding landscape, responding negatively to the extent of agricultural land and positively to natural and semi-natural lands (Kennedy et al. 2013, Senapathi et al. 2017). The effects of landscape configuration, the spatial arrangement of habitat patches within a landscape, on pollinators remain less clear (Hass et al. 2018). In heavily modified, fragmented landscapes, pollinators are more likely to encounter habitat edges (Fahrig 2003). Habitat edges may facilitate or impede pollinator movement throughout a landscape and can have varying effects on pollinator distributions and abundance (Hadley and Betts 2012). On one hand, edges are frequently ecologically distinct compared to the patch interiors (Ries et al. 2004), and in agricultural landscapes, edges can provide important foraging resources and nesting sites for pollinators (e.g. bumble bees; Svensson et al. 2000, Kells and Goulson 2003, Pywell et al. 2005). On the other hand, flower visitors (e.g. butterflies; Ries and Debinski 2001, Schtickzelle et al. 2006, Mair et al. 2015) have been demonstrated to be less likely to cross habitat boundaries, potentially affecting colonization and persistence within highly modified landscapes. Even within the same landscape, the responses of flower visiting insects to habitat edges can be taxon-specific (Ries and Debinski 2001, Holzschuh et al. 2010).

Because of pollinators' complex and multi-scale responses, studies that address the drivers of pollinator community structure at focal sites must consider both the site-scale provisioning of resources and the landscapes within which focal sites are situated (Kremen et al.

2007). However, our understanding of the varied, multi-scale drivers of pollinator community structure remains underdeveloped, especially with respect to many non-bee pollinators (Grass et al. 2016, Senapathi et al. 2017).

We assessed potential drivers of insect flower visitor structure on remnant and reconstructed ("restored" on former crop fields) tallgrass prairies in the agricultural landscapes of northeast Kansas, USA. Our previous work in this system revealed that flower visitor diversity and abundance were comparable across remnant and reconstructed prairies (Denning and Foster 2018; dissertation Chapter 1) but did not assess potential multi-scale drivers of flower visitor communities. Herein, we evaluated relationships between flower visitor community structure (richness, diversity, and composition) and both site-scale forb communities (richness, abundance and composition) and landscape-scale composition and configuration in the tallgrass prairie ecosystem. Grasslands comprise 37% of global terrestrial land cover and play an integral role in global food security yet have been subject to extensive degradation and agricultural conversion (O'Mara 2012). The tallgrass prairie is North America's most threatened ecosystem, having lost extensive land cover to agricultural conversion (Samson and Knopf 1994). Remnant and reconstructed prairies are often small and embedded within highly modified landscapes. Taken together, this lends particular urgency to improving our understanding of tallgrass prairie pollinator communities.

We used a highly taxonomically resolved dataset to evaluate local and landscape-scale correlations involving the entire flower visitor community, as well three subgroups —bees, butterflies, and syrphid/bombyliid flies. Our focus on bees was driven by their global importance as pollinators. Butterflies are less efficient pollinators in temperate ecosystems (Cane 2001) but are a diverse group of pollinators globally (Ollerton 2017), and their relative ease of

identification could make them useful indicators of suitable pollinator habitats (Thomas et al. 1992). Syrphid and bombyliid flies (Diptera:Syrphidae, Bombyliidae) can be important pollinators (Larson et al. 2001) but, like many non-bee pollinators, they are often overlooked by researchers (Rader et al. 2016). We hypothesized that (1) flower visitor α-diversity would be significantly associated with site-scale forb α-diversity and abundance; (2) sites more similar in forb composition would also be more similar in flower visitor composition; (3) flower visitor α-diversity would be positively associated with the extent of native grasslands in the surrounding landscapes, as well as the combined extent of native grasslands and woodlands (together, considered "natural/semi-natural" lands); (4) given the highly modified nature of the surrounding landscapes, associations involving flower visitor α-diversity and the extent of habitat edges in these landscapes would be largely negative, but may be taxon-specific; and (5) that butterflies would be appropriate proxies for the associations of other flower visitor groups with site- and landscape-scale factors.

Methods

Sampling Methods

The study was conducted in the tallgrass prairie-eastern deciduous forest ecotone of northeast Kansas, USA. From 2013-2015, we surveyed forbs and flower visiting insects across ten tallgrass prairies located within 120 km of Lawrence, Kansas (38.97° N, 95.24° W; Fig. 1.1 in Chapter 1). Sites ranged in size from 3.1 to 7.0 ha (mean $\pm$ 1 SE: 4.71$\pm$ 0.40 ha). Study sites at least 5 km from one another were chosen, such that flower visitors were likely unable to travel between sites. The sites consisted of five remnant (never-plowed) prairies and five prairies reconstructed on former crop fields. Detailed information about the study sites and sampling methods can be found in Denning and Foster (2018) (dissertation Chapter 1). Flower visitors

were recorded at each site using a two-stage sampling approach consisting of 60 minutes of timed sampling in a 100 x 100 m study plot placed near the center of each site, as well as sampling along four belt transects measuring 20 x 2.6 m each. For both sampling methods, we recorded all insects observed to be in contact with the reproductive structures of open flowers, as well as the species identity of the forb each insect was visiting. Because pollen transfer was not explicitly assessed, we refer to the insects as flower visitors, rather than pollinators. Independent estimates of the floral abundances of currently-flowering forbs, measured as the size of the floral display (cm^2), were also recorded during each transect walk. Sites were surveyed from the onset of flowering in spring until late July, when most sites were hayed or mowed. Sites were surveyed 2-4 times annually, depending on weather and the timing of management practices. After each survey, insects were freeze-killed and mounted in the laboratory. Numerous entomologists assisted with insect identification (see Acknowledgements). Voucher specimens are housed in the California State Collection of Arthropods and the Snow Entomological Collection at the University of Kansas.

Landscape Composition

We characterized land use within 1 km of the study sites' boundaries. Baseline data were obtained from the 2005 Kansas Land Cover Patterns-Level IV raster (KLCP; Kansas Applied Remote Sensing Program 2010). We then used two methods to account for land use changes that occurred after the KLCP raster was published. First, we updated agricultural land use, when necessary, using the 2014 Cropland Data Layer (CDL; USDA National Agricultural Statistics Service 2014). We also visually surveyed all accessible grasslands within 1 km of the study sites to distinguish between two grassland types: warm-season and cool-season, so called because of the respective dominance of grasses utilizing the warm-season (C4) and cool-season (C3)

photosynthetic pathways. In this region, both warm- and cool-season grasslands are commonly managed for forage production as pastures or hayfields (Questad et al. 2011). Warm-season grasslands are typically characterized by native grasses (Jog et al. 2006), and many warm-season grasslands (e.g. remnant prairies, high quality reconstructed prairies) are forb diverse, likely making them suitable pollinator habitats. In contrast, cool-season grasslands are typically found on formerly tilled lands and are dominated by introduced C3 grasses (Foster et al. 2009). Cool-season grasslands are usually subject to intensive inputs, including annual fertilization and broadleaf herbicide application (Questad et al. 2011) and may be less suitable for pollinators. We did not directly measure the landscape-scale provisioning of floral resources, and it is possible that some cool-season grasslands may indeed be providing important foraging and/or nesting resources for pollinators. Likewise, some warm-season grasslands may be providing few such resources, depending on past land use history and current management practices. A final raster layer of 30 x 30 m resolution was created using the KLCP raster, updated with the CDL data and the visual surveys of grasslands.

We identified three landscape variables of interest: the proportion of warm-season grasslands, the proportion of natural/semi-natural (NSN) lands, and the extent of NSN and warm-season grassland habitat edges, measured as edge density. We defined NSN lands as the combined extent of warm-season grassland and woodland. Landscape composition measures were calculated exclusive of the land cover class "water". We deliberately considered both NSN lands and warm-season grasslands (a component of NSN lands) because, with the exception of spring ephemeral forbs, deciduous forests provide relatively few floral resources (Winfree et al. 2007). Edge density was calculated in FRAGSTATS version 4.2 (McGarigal et al. 2012) and equals the sum of the lengths of all edge segments of the focal land cover type, divided by the

total landscape area. We calculated landscape measures at two spatial scales surrounding, but not including, each site – 250 m and 1 km. The spatial scales at which pollinators respond to landscape structure have varied widely across multiple studies (Steffan-Dewenter et al. 2002, Kremen et al. 2004, Hines and Hendrix 2005, Bates et al. 2011, Grass et al. 2013), and this variation likely reflects both the unique aspects of the study ecosystems and the distinctive life history traits of the focal pollinator groups. We chose to utilize a relatively small spatial scale (250 m) that primarily incorporated the fields directly adjacent to the study sites, as well as the largest spatial scale feasible (1 km) given our visual surveying of grasslands. These spatial scales are comparable to those typically used in landscape-scale studies of pollinators (see citations above).

Statistical Analyses

Analyses were conducted in R version 3.3.2 (R Core Team 2016). Species richness was rarefied to nine total samples using the R package 'rich' (Rossi 2011), to account for differences in sampling effort. Floral display size for all forbs in-flower at the time of sampling (hereafter referred to as forb abundance) was rarefied in the same manner. Diversity was calculated as the effective number of species ($e^{H'}$; Jost 2006). Richness, abundance and diversity were all calculated as a single cumulative value from 2013-2015. Prior to conducting the main analyses, we assessed the forb and flower visitor composition data for spatial autocorrelation using Mantel tests based on the geographic distance between sites (Bray-Curtis dissimilarity; n = 999 permutations). No spatial autocorrelation was found for the forb community or any of the four focal insect groups, so we proceeded with the main analyses without explicitly accounting for the distance among sites. Because our sites were sampled intensively for multiple years, we were only able to sample ten total sites. Therefore, we analyzed the effects of site-scale forb

community structure and landscape composition and configuration separately to avoid over-parameterizing the statistical models. Because our previous work did not find significant differences in flower visitor diversity between remnant and reconstructed prairies, we did not include a term to distinguish between these site types in our models (see Denning and Foster 2018; dissertation Chapter 1).

Site-Scale Analyses

We used correlation tests (Pearson's correlation coefficient) to assess whether the diversity or richness of the four focal insect groups was significantly associated with forb richness. Because forb abundance was not normally distributed (Shapiro test, $P = 0.0341$), we used Spearman's rank correlation coefficient to examine associations involving forb abundance. Rather than calculating forb diversity directly, we evaluated the two components of forb diversity (richness and abundance) separately, as each of these factors may have separate and complementary associations with flower visitor structure. Next, we assessed whether the species composition of the focal insect groups was significantly associated with forb species composition across the sites. We performed a Procrustes test on the non-metric multidimensional scaling ordinations (Bray-Curtis dissimilarity) of the forb and insect relative abundance data. The forb matrix was used as the reference matrix, and the significance of the concordance between the forb community and each focal insect group was assessed iteratively via the PROTEST function in the R package 'vegan' (Peres-Neto and Jackson 2001, Oksanen et al. 2017). A significant Procrustes result indicates that sites more similar in forb community composition are also significantly more similar in flower visitor composition.

Networks of interacting plants and pollinators typically exhibit a core group of abundant, generalist species (Bascompte and Jordano 2007). Upon finding significant concordance between

the forb and flower visitor communities (see Results), we evaluated whether this was due to a small number of highly abundant flower visitors. We first tallied the most frequently observed plant-flower visitor interactions across all sites and years. We then removed individual insects involved in the five, 10, and 15 most frequently observed interactions, and, for each removal scenario, re-ran the Procrustes test. In all three removal scenarios, the Procrustes goodness-of-fit statistic (m^2) increased, compared to the observed m^2 for the full dataset (see Results), indicating weaker concordance between communities. We evaluated the significance of the increase in m^2 using a randomization procedure; for each removal scenario, we randomly removed the same number of insect individuals from the dataset and recalculated m^2 (n = 999 iterations). *P* values were calculated by comparing our observed m^2 values to the null distribution of m^2 values in a one-tailed test, where a significant *P* value indicates that removing the insects involved in the most frequently-recorded interactions causes significantly more discordance in community composition than randomly removing the same number of insects.

Landscape-Scale Analyses

For each spatial scale, we first assessed whether the proportion of NSN lands and the proportion of warm-season grasslands were significantly correlated. We also assessed whether the proportion of either land use type was significantly associated with the edge density of that same land use type. We then performed correlation tests (Pearson's correlation coefficient) to assess whether the richness or diversity of the four focal insect groups was significantly associated with any of the remaining measures of landscape composition or configuration. Upon finding significant correlations involving warm-season grassland edge density at the 250 m scale (see Results) we used the updated KLCP raster layer to estimate the extent of each land cover class directly abutting these edges.

Results

Overview

Ninety-nine surveys were conducted, yielding 6679 records of 326 insect taxa visiting 127 forb taxa. We identified 85% of flower visitors to species (97% resolved to genus-level or finer). We identified 89% of all forbs to species, and 97% to genus or finer. The flower visitor community was comprised of 33% coleopterans, 33% hymenopterans, 15% dipterans, 14% lepidopterans, 4% hemipterans, and <0.01% "other/unidentified", based on abundances of individuals. We recorded 2021 bees (91 species), 853 butterflies (43 species), and 830 syrphid and bombyliid flies (24 species). For a list of flower visitor species, see Table S1.2 in Appendix 1. See Table 2.1 for landscape composition and configuration summary statistics.

Site-Scale Forb Communities

Bee diversity was significantly, positively associated with forb richness ($r = 0.864$, $P = 0.001$; Fig. 2.1A). No other measures of richness or diversity for the four insect groups were significantly associated with forb richness ($P > 0.05$; Fig. S2.1 in Appendix 2). Similarly, there were no significant correlations involving forb abundance ($P > 0.05$; Fig. S2.2). There was a significant association between forb composition and that of the entire flower visitor community ($m^2 = 0.60$, $P = 0.039$). As is typical for surveys of a wide variety of taxa (Preston 1948, Andrewartha and Birch 1954), including pollinators (Williams et al. 2001), the flower visitor community was comprised of a small number of very abundant species and a large number of infrequently-recorded species. Flower visitor individuals involved in the five, 10 and 15 most frequently recorded interactions comprised 15%, 23% and 29% of all insects observed (Table S2.1). The Procrustes goodness-of-fit statistic (m^2) increased with the removal of insect individuals involved in the five- ($m^2 = 0.71$), 10- ($m^2 = 0.73$) and 15 ($m^2 = 0.70$) most frequently

recorded interactions. However, for all removal scenarios, the decrease in concordance resulting from the removal of these insects was not significantly greater than the decrease in concordance resulting from randomly removing the same number of insects. Procrustes tests involving the three flower visitor subgroups were non-significant ($P > 0.05$).

Landscape Context

The a priori comparisons of landscape variables yielded two significant correlations. At the 250 m scale, the proportion and edge density of NSN lands were significantly, negatively correlated (r = -0.694, $P = 0.026$). At the 1 km scale, the proportion and edge density of warm-season grasslands were significantly, positively correlated (r = 0.733, $P = 0.016$). We therefore excluded the above two edge density measures from further analyses, with the understanding that significant relationships involving the variables they were correlated with might be attributable to these factors.

There were no significant correlations involving the richness or diversity of the entire flower visitor community and any landscape variable. However, there were several positive associations involving the three focal subgroups of insects. Bees and flies were largely positively associated with the extent and edge density of warm-season grasslands at both spatial scales. At the 250 m spatial scale, bee diversity was significantly positively correlated with both the proportion of warm-season grasslands (r = 0.756, $P = 0.011$; Fig. 2.1B) and the edge density of warm-season grasslands (r = 0.642, $P = 0.045$; Fig. 2.1C); bee richness was marginally significantly, positively associated with warm-season grassland edge density (r = 0.553, $P = 0.097$). At this spatial scale, woodlands and cool-season grasslands were the primary land use categories bordering warm-season grasslands—72% of the raster cells abutting warm-season grasslands were categorized as woodland and 16% were categorized as cool-season grassland. At

the 1 km scale, bee diversity was significantly, positively associated with the proportion of warm-season grasslands (r = 0.775, *P* = 0.009; Fig. 2.1D). At the 250 m scale, syrphid/bombyliid fly diversity was significantly, positively associated with the edge density of warm-season grasslands (r = 0.728, *P* = 0.017; Fig. 2.1E) and marginally, positively associated with the proportion of warm-season grasslands (r = 0.549, *P* = 0.100). In contrast, butterflies were correlated only with measures of NSN lands. Butterfly richness was marginally significantly, positively associated with the proportion of NSN lands within 250 m (r = 0.613, *P* = 0.060) and was significantly, positively associated with the proportion of NSN lands within 1 km (r = 0.760, *P* = 0.011; Fig. 2.1F). Butterfly diversity was marginally, positively associated with the edge density of NSN lands (r = 0.580, *P* = 0.079) within 1 km.

Discussion

Despite pollinators' global importance, conservation and restoration of pollinators remains challenging because of their species- and life history diversity. Our work indicates that site-scale forb composition may play a strong role in structuring flower visitor communities and thus could be a useful indicator for the composition of the diverse assemblage of flower visitors in this system. In addition, our results indicate that in the tallgrass prairie ecosystem, where focal remnant/reconstructed prairies are often small and isolated from one another, landscape context may play a stronger role in driving flower visitor community structure than site-scale forb α-diversity and floral abundance. Moreover, our work highlights the need to consider pollinators' responses to different types of natural and semi-natural lands within focal landscapes, and the taxon-specific responses of butterflies, bees and flies in our study suggest that caution should be taken when using butterflies as indicators of the responses of other pollinators to site- and landscape-scale factors in the tallgrass prairie ecosystem.

Site-scale Associations

Although strong correlations between forb and flower visitor α-diversity and abundance have been observed across many ecosystems, these relationships were largely absent in our study, with the exception of bees. Weak, non-significant or saturating relationships between forb and flower visitor α-diversity have been observed in other temperate grasslands and agri-ecosystems (Hegland and Boeke 2006, Ebeling et al. 2008, Grass et al. 2016), and landscape context can disrupt local associations between plant and flower visitor diversity (Dainese et al. 2017). In the tallgrass prairie, our results corroborate those of Davis et al. (2008), who found that forb diversity was not significantly associated with that of butterflies or bees, and with Shepherd and Debinski (2005) who did not find significant correlations between butterfly richness or abundance and plant diversity. Our results suggest that cross-taxon congruence in α-diversity is likely context dependent, making it unwise for conservation practitioners in the tallgrass prairie ecosystem to rely solely upon site-scale forb α-diversity or abundance as a predictor of pollinator diversity. It is important to note that in our study, bees were more than twice as frequently recorded, compared to butterflies or syrphid/bombyliid flies. Therefore, the weak correlations involving the latter two groups could be largely due to sample size differences. However, correlations involving the entire flower visitor community were also non-significant, suggesting that the observed weak associations involving the butterfly and fly subgroups may indeed have a biological basis. At our sites, many flower visitors may be limited by non-floral food resources. For example, many butterflies utilize nutrient sources (e.g. tree sap, dung) that we did not measure and that may not correlate strongly with forb richness or abundance. In addition, several butterfly species we collected rely on non-forb species as caterpillars (e.g. grass skippers in the subfamily Hesperiinae), and we did not assess grass abundance or diversity at our sites. The

positive bee-forb relationship may be attributable to bees' sole nutritional reliance on floral resources. Non-food resources (e.g. the availability of nesting space and materials) may also limit flower visitor populations at our sites.

Despite the weak and taxon-specific responses of flower visitors to forb richness and abundance, we observed strong congruence between forb composition and that of the entire flower visitor community. Our species-removal simulations indicated that this was not attributable solely to a small number of abundant generalist species, but rather was likely due to the interactions of a large number of less frequently recorded species. The complete flower visitor dataset was comprised of largely of non-bee taxa, which are not typically targets of conservation and monitoring schemes. As such, the congruence that we observed across a diverse array of flower visitors and forbs may be particularly useful for practitioners seeking to conserve these oft-neglected species. One of the major challenges associated with insect monitoring and conservation is accounting for the vast taxonomic and life history diversity of insects (Shuey 2013). Our results suggest that practitioners seeking to monitor the diverse tallgrass prairie flower visitor community may be able to utilize forb composition data, which is typically much easier to obtain, to make inferences about the flower visiting insect species present at a focal prairie.

Landscape-scale Associations

Landscape context was more strongly correlated with the α-diversity of flower visitor groups than site-scale forb abundance or diversity. Associations between flower visitors and landscape composition were highly taxon-specific. The positive association between butterflies and NSN lands, but not warm-season grasslands considered independently, may indicate that both components of NSN lands are contributing complementary sets of foraging and/or nesting

resources for these taxa. Indeed, many of the butterfly species we recorded are habitat generalists, known to inhabit prairies as well as woodlands and woodland edges in this region; a subset of these taxa also utilize woody species as caterpillar host plants (Betros 2008). In contrast, bees' positive association with only the warm-season grassland component of surrounding NSN lands suggests that woodlands are providing comparatively few resources for bees in this system. Aside from a spring blooming period, woodlands in this region have relatively low levels of floral abundance. Additionally, we recorded relatively few obligate cavity nesting bees (some of which nest in pre-existing holes in wood) and a large number of ground nesting bees, suggesting that among our study sites even the landscapes with the lowest extent of surrounding woodlands are providing sufficient nesting resources for these species. Taken together, these results lend additional support to the importance of distinguishing among multiple types of natural and semi-natural lands when examining potential drivers of flower visitor communities and when formulating conservation and restoration plans (Cole et al. 2017). For practitioners selecting focal sites for prairie restoration with the goal of conserving or reinstating bees, our results suggest that prioritizing focal sites within landscapes that contain higher amounts of warm-season grasslands within 1 km may be more beneficial than selecting sites embedded in a more wooded landscape matrix. In contrast, practitioners seeking to conserve butterfly communities within this system would likely benefit from selecting focal sites embedded in landscape matrices containing a greater extent of woodlands.

Landscape configuration is likely to have complex, context- and taxon-dependent effects on flower visitors (Hadley and Betts 2012). Whereas Kennedy et al.'s (2013) meta-analysis indicated only weak effects of landscape configuration on bees, several studies have shown that many flower visitors do indeed respond to aspects of landscape configuration, including patch

density, edge density, and patch perimeter:area ratio (Holzschuh et al. 2010, Hopfenmüller et al. 2014, Perović et al. 2015). Our results indicate that in the tallgrass prairie, landscape configuration may be an important driver of flower visitor structure. At the 250 m scale, bee and fly diversity were both positively associated with warm-season grassland edge density, and our follow-up characterization of these edges indicated that warm-season grasslands primarily bordered woodlands. Plant community composition and abiotic factors at forest edges have been shown to differ from that of the forest interior (Matlack 1994, Murcia 1995). It is therefore possible that these grassland-woodland ecotones are providing valuable foraging resources, nesting materials and/or nesting microhabitats for these groups. Unfortunately, we were unable to directly assess the effects of grassland-woodland edge density on flower visitor communities, as this measure was highly correlated with the extent of both NSN lands and warm-season grasslands. Our findings highlight the need for future work in the tallgrass prairie ecosystem that explicitly focuses on the potential utility of grassland-woodland habitat edges in supporting pollinator communities.

Cross-taxon Comparisons

The three focal subgroups of flower visitors in this study exhibited several notable differences in their associations with site-scale forb communities as well as the composition and configuration of lands in the surrounding landscapes. Therefore, our hypothesis that butterflies would be appropriate proxies for the associations of other flower visitor groups to both local- and landscape-scale factors was not supported. Despite the relative ease of butterfly identification, our results suggest that practitioners in the tallgrass prairie ecosystem should proceed with great caution when utilizing butterfly community structure to draw inferences about the status of other flower visitor groups. Two important caveats should be noted. First, because we only sampled

ten sites, it is possible that our conclusions are being affected by relatively low statistical power. Future work in this system should focus on examining the multi-scale drivers of flower visitor community structure across a wider range of remnant and reconstructed prairie sites. Second, our study focused on the entire butterfly community, which included a large number of habitat generalists. It is possible that the responses of the grassland specialist butterfly assemblage would more closely mirror that of other flower visitor groups. Ultimately, care should be taken when extending our results to other ecosystems and geographical regions; butterflies' usefulness as correlates of the richness or abundance of other groups appears to be highly context dependent (Fleishman and Murphy 2009).

Conclusions

As human-mediated pressures on Earth's remaining natural and semi-natural lands continue to increase, it becomes increasingly critical to understand pollinators' responses to habitat degradation, loss and restoration. We found that flower visitors' associations with site-scale provisioning of floral resources and landscape-scale land use are multifaceted, differing greatly in their strength and direction both among taxa and across spatial scales. Our results indicate that practitioners in the tallgrass prairie ecosystem should be cautious about relying solely on site-scale forb α-diversity to draw inferences about the diversity of many flower visitor taxa; nevertheless, forb composition may be valuable for predicting flower visitor composition in this system. In addition, when feasible, the selection of focal tallgrass prairie sites for pollinator restoration within these human-modified landscapes should take into account both landscape composition and configuration, with the understanding that different pollinator groups in this system may benefit from different landscape contexts.

Figures and Tables

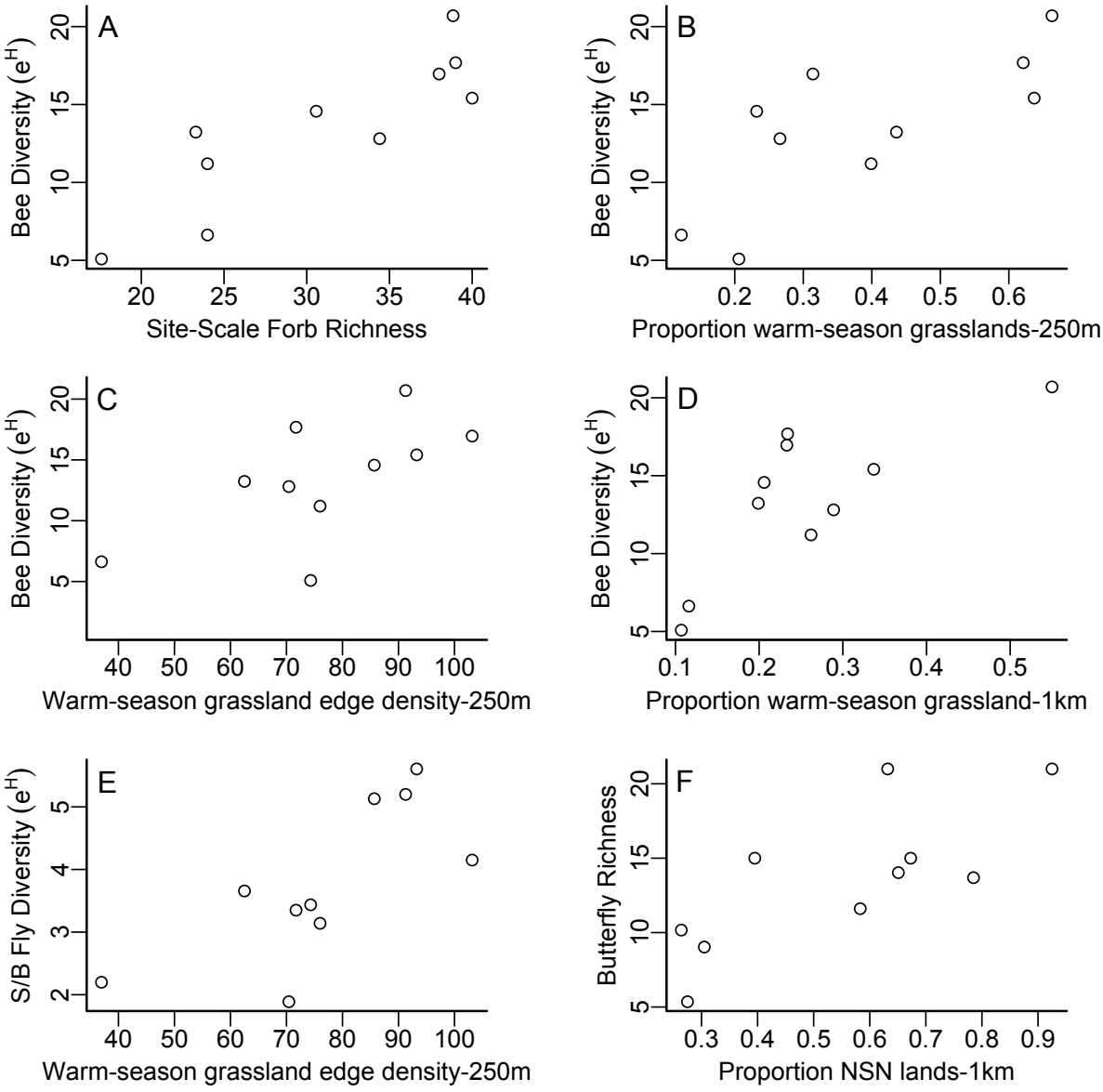

Figure 2.1. Significant correlations between **A)** bee diversity and forb richness measured at 10 tallgrass prairie study sites; **B)** bee diversity and the proportion of warm-season grasslands within 250 m of the sites; **C)** bee diversity and warm-season grassland edge density within 250 m of the sites; **D)** bee diversity and the proportion of warm-season grasslands within 1 km of the sites; **E)** syrphid/bombyliid (S/B) fly diversity and warm-season grassland edge density within 250 m of the sites; **F)** butterfly richness and the proportion of natural and semi-natural (NSN) lands within 1 km of the sites. Richness values were rarefied using sample-based rarefaction to nine total samples across each site.

Table 2.1. Mean values ± 1 SE for land use and configuration within 250 m and 1 km of tallgrass prairie study sites. NSN = natural/semi-natural lands, and consisted of the sum of warm-season grasslands and woodlands surrounding the sites. Edge density is measured as (m ha^{-1}).

	250 m scale	1 km scale
Proportion NSN	0.78 ± 0.05	0.55 ± 0.07
NSN edge density	38.30 ± 9.78	47.31 ± 6.34
Proportion warm-season grassland	0.39 ± 0.06	0.25 ± 0.04
Warm-season grassland edge density	76.53 ± 5.89	50.99 ± 6.55

Chapter 3: Plant-pollinator networks exhibit similar structural properties and robustness to simulated species loss on remnant and reconstructed tallgrass prairies

Abstract

Biotic interactions play a fundamental role in structuring Earth's ecosystems. One such interaction, animal-mediated pollination, is both critical to maintaining terrestrial biodiversity and key to ensuring global food security. Unfortunately, pollinators, and thus, the interactions they participate in, face numerous anthropogenic threats. Despite the utility and popularity of using a network approach to examine plant-pollinator interactions, few researchers have examined whether habitat restoration practices can successfully reinstate the structure of plant-pollinator networks. Herein, we used a highly taxonomically resolved dataset comprising nearly 7000 records of interactions between forbs and flower visiting insects to evaluate whether network architecture and robustness to species loss have been reinstated across tallgrass prairies in Kansas, USA, that have been reconstructed on former crop fields. We found that reconstructed prairie networks were structurally similar to those of reference, remnant prairies. All networks were significantly non-nested, modular and specialized, indicating that interaction partitioning is a fundamental feature of these networks. In addition, shared forb and flower visitor taxa exhibited similar interaction specialization across both types of prairie. Furthermore, networks were highly robust to simulated species loss. Taken together, our work suggests that habitat restoration practices in this system have succeeded in restoring functioning networks of plants and flower visiting insects.

Introduction

Biotic interactions are a fundamental component of ecosystems, and a wealth of ecological functions are mediated by plant-animal interactions (McCann 2007, Schleuning et al. 2015). One critical type of biotic interaction in terrestrial ecosystems is pollination. Animal-mediated pollination is integral to the maintenance of terrestrial biodiversity, and global food security relies on pollination services (Klein et al. 2007, Ollerton 2017). Traditionally, studies of plant-pollinator mutualisms have focused on species-specific, highly coevolved interactions (e.g. yuccas and yucca moths; figs and fig wasps) or have concentrated on a subset of the plant and pollinator communities (Burkle and Alarcón 2011). However, in recent years, researchers have discovered the value of using a network approach to investigate mutualistic interactions, including plant-pollinator interactions, in the context of entire communities (Proulx et al. 2005, Forup et al. 2008). Plant-pollinator networks provide a framework for examining the community-wide interactions between plants and their floral visitors, and studying the architecture of these networks can yield valuable information about the structure and functioning of biological communities (Schleuning et al. 2015). Our understanding of the pervasive features of these networks continues to grow: mutualistic networks have traditionally been considered highly nested, with specialist species interacting with proper subsets of the species generalists interact with (Bascompte et al. 2003, but see Staniczenko et al. 2013). Networks are often modular, consisting of subgroups of species that interact frequently with one another but less commonly with members of other modules (Olesen et al. 2007) and are characterized by species connectivity distributions in which most species have few interaction partners and a small number of species have many interaction partners (Jordano et al. 2003).

The human-mediated threats facing pollinators lend particular urgency to improving our understanding of the structure and functioning of plant-pollinator networks. These anthropogenic pressures include habitat loss and degradation, pesticide use and global climate change (reviewed by Potts et al. 2010). Ecological degradation resulting from human activities threatens not only species diversity, but disrupts plant-pollinator interactions. As such, it is imperative that the focus of restoration efforts be placed not solely on re-establishing species diversity but also on reinstating these complex biotic interactions (Society for Ecological Restoration International Science & Policy Working Group 2004, Menz et al. 2011). Nevertheless, despite the utility of the plant-pollinator network approach, few studies have assessed the extent to which ecological restoration reinstates pollinator communities and impacts network architecture (Kaiser-Bunbury and Blüthgen 2015, Kaiser-Bunbury et al. 2017)

In this study, we used a highly taxonomically-resolved dataset comprising nearly 7000 plant-pollinator interactions to compare plant-pollinator network structure between five remnant (never plowed) tallgrass prairies and five prairies reconstructed ("restored") on former cropland. North America's tallgrass prairie ecosystem has been subjected to widespread agricultural conversion, such that in Kansas, where this study took place, less than 18% of the pre- Euro-American settlement tallgrass prairie remains (Samson and Knopf 1994). Our previous work in this system demonstrated that forb diversity and composition differ substantially between remnant and reconstructed prairies, but that these differences do not extend to insect flower visitors (Denning and Foster 2018; dissertation Chapter 1). In addition, the composition and configuration of the landscapes surrounding these relatively small prairies appears more central in governing flower visitor community structure than does site-scale provisioning of floral resources (Denning and Foster *in press*, Biological Conservation; dissertation Chapter 2).

Although the number of descriptors of network topology is ever-growing, we focused our analyses on a set of six network properties identified as having implications for ecological degradation, conservation, and restoration (Memmott et al. 2004, Forup et al. 2008, Tylianakis et al. 2010, Nielsen and Totland 2014, Kaiser-Bunbury and Blüthgen 2015, Ribeiro da Silva et al. 2015, Soares et al. 2017): network size, network-level specialization (H_2'; Blüthgen et al. 2006), nestedness, modularity, networks' robustness to simulated species removal, and the species-level interaction specialization (d'; Blüthgen et al. 2006) of plant and animal taxa shared among remnant and reconstructed prairies. If prairie reconstruction has successfully reinstated pollinator communities, we predict that network size, network-level specialization, nestedness, and modularity would be similar across remnant and reconstructed prairies, with networks across both types of prairie exhibiting similarly high robustness to simulated species loss. However, ecological restoration, including that of prairies (Kindscher and Tieszen 1998, Kurtz 2013), is challenging for a number of biological and logistical reasons. If restoration practices have not succeeded in reinstating functioning pollinator communities, several alternative predictions regarding network architecture can be made. Networks may be smaller across unsuccessfully reconstructed prairies, due to a failure of forb and/or flower visitor species to successfully access or colonize the sites. Ecological restoration has been linked to increases in network-level specialization, suggesting that network complexity increases in response to restoration (Marerro et al. 2014, Ribeiro da Silva et al. 2015, but see Kaiser-Bunbury et al 2017). Therefore, unsuccessfully reconstructed prairie networks may exhibit lower H_2' values than those of reference, remnant prairies. Increasing nestedness and modularity have been associated with larger networks (Olesen et al. 2007, Moriera et al. 2015), suggesting that small, unsuccessfully reconstructed prairies could be less nested and modular than remnants. Because both nestedness

and modularity are thought to enhance the stability of networks (Krause et al. 2003, Memmott et al. 2004), unsuccessfully-reconstructed prairies may have less stable plant-pollinator networks compared to prairie remnants, and these networks may thus be less robust to species removal.

If species that are recorded across both remnant and reconstructed prairies (i.e. "shared species") largely exhibit similar levels of specialization between the two types of prairie, this could be indicative the success of habitat restoration efforts, whereas variation in specialization that is independent of restoration history could simply be reflective of the spatial and temporal heterogeneity that often characterizes plant-pollinator interactions (Moeller 2005, Petanidou et al. 2008, Nielsen and Totland 2014). Alternatively, systematic differences in species-level specialization at remnant versus reconstructed prairies may signify fundamental differences in the structure or functioning of forb and flower visitor communities as a consequence of habitat degradation and subsequent restoration, and could inform future conservation and management decisions in this system.

Methods

Site Information

We conducted this study across ten tallgrass prairies in the tallgrass prairie-eastern deciduous forest ecotone of northeast Kansas (Fig. 1.1 in Chapter 1). The Anderson Family Prairie (AND), Guess Prairie (GUE), Rockefeller Prairie (ROC), Snyder Prairie (SNY) and Teal Lake Prairie (TEA) are remnant, never-plowed tallgrass prairies. Baker Farm (BAK), Busby Prairie (BUS), Byers Family Prairie (BYE), Coombs Prairie (COO), and Kettle-Look Prairie (KET) are prairies "reconstructed" (Kurtz 2013) on former crop fields. Sites ranged from 3.1-7.0 ha (all sites mean $\pm$ 1 SE: 4.71 $\pm$ 0.40 ha; remnants: 4.64 $\pm$ 0.48 ha; reconstructed sites: 4.78 $\pm$ 0.69 ha) and were located at least 5 km away from one another, making it unlikely that

individual insects would travel between sites. The reconstructed prairies in this study ranged in age from 4-21 years and were seeded with native forbs and grasses by the landowners. Sites were burned or hayed at least once during the study, with the exception of BYE.

Sampling Methods

We surveyed forbs and flower visiting insects 2-4 times annually at each site from 2013-2015. Surveys took place from late April/early May until late July, when several sites were hayed. Detailed descriptions of the study sites and sampling methods can be found in dissertation Chapter 1. Flower visitor surveys consisted of a two-stage approach: a 60 minute bout of opportunistic sampling of flower visitors within a 100 x 100 m study plot situated near the site's center, followed by non-timed sampling along four 20 x 2.6 m belt transects. During these surveys, all insects greater than approximately 2 mm in size that were observed to be in contact with floral reproductive structures were recorded. When feasible, insects were netted and placed individually into vials labelled with the forb species each insect was visiting. During each survey, we also collected independent estimates of the abundances of currently flowering forb species. To do this, we walked each belt transect, recording the species identities of all forbs currently in bloom. Forb abundance was measured as the total size of the floral display across all belt transects (20 m x 2.6 m x 4 transects = 208 m^2 total sampling area) and was recorded by placing a clear, plastic grid over each open inflorescence and measuring floral display size in cm^2. Insect identifications were carried out with the assistance of many taxonomists (see Acknowledgements). Voucher specimens are housed in the California State Collection of Arthropods (Diptera only) and the Snow Entomological Collection at the University of Kansas.

Visualization of Plant-Pollinator Networks

A single plant-pollinator network was generated for each site, which consisted of all interactions recorded between forbs and flower visitors from 2013-2015. While it can be problematic to include multiple survey dates in a single network, our relatively short sampling season (approximately 12 weeks per year) likely limited the extent of "forbidden links" (Jordano et al. 2003) due to phenological mismatches in our system. Furthermore, because sites were typically surveyed only 3-4 times per year, combining network data across study years yielded a more complete, species-rich picture of the interactions among plants and flower visitors. We generated networks and calculated network metrics using *bipartite* version 2.08 (Dormann et al. 2008, Dormann et al. 2009, Dormann 2011) in R version 3.3.2 (R Core Team 2016). All subsequent analyses were also conducted in R. Despite referring to individual insects as "flower visitors", in keeping with convention, we use the term plant-pollinator network to refer to these networks.

Network Metrics and Statistical Analyses

Because network metrics can be influenced by sampling effort, we first assessed whether sampling effort was comparable across remnant and reconstructed prairies by comparing the total number of site visits between the two types of prairie using a linear model. We then assessed whether network size, network-level specialization, nestedness, robustness to species removal, and species-level specialization of shared animal (A) and plant (P) taxa differed between remnant and reconstructed prairies. Network size has been measured both multiplicatively, representing the size of the interaction matrix, and additively, representing the total species richness of plants and animals in a network (e.g. Albrecht et al. 2010, Trøjelsgaard and Olesen 2013). Therefore, we measured network size as both A x P and A + P, where A and P represent animal and plant species richness, respectively. The degree of network-level specialization was

assessed using H_2' (standardized two dimensional Shannon entropy), a measure that describes the extent to which interactions deviate from expectations based on species abundances (Blüthgen et al. 2006). H_2' ranges from 0 to 1, with higher levels of H_2' indicating greater specialization and niche partitioning across species in a focal network (Blüthgen et al. 2006). Nestedness was calculated using weighted NODF, which takes into account species abundance data (WNODF: Almeida-Neto and Ulrich 2011). WNODF ranges from 0 to 100, with higher values indicating greater nestedness (Almeida-Neto and Ulrich 2011). Randomization tests (n = 1000 replicates), using Patefield's null model (Patefield 1981), were used to test whether each network was significantly specialized and, separately, whether each network was significantly nested. This conservative null model approach randomizes species interactions while keeping species frequencies (row and column totals) fixed (Blüthgen et al. 2008) and was carried out using the *r2dtable* function in R. We calculated normalized modularity (Q^{norm}; Beckett 2016) for each network using the *DIRT_LPA_wb_plus* function and the online supporting R code from Beckett (2016). We tested whether each network was significantly modular using the null model approach outlined above, with 500 replicates. Differences in network size, H_2', WNODF and Q^{norm} between networks from remnant and reconstructed sites were assessed using linear models.

We performed extinction simulations to assess whether networks from remnant sites were more robust to species loss than networks from reconstructed sites. Extinction simulations were modelled after those performed by Memmott et al. (2004) and Forup et al. (2008). Simulations were performed using the *second.extinct* function in bipartite, and involved removing insect species one at a time from a network. After an insect species was removed, any plant species left unlinked was also removed from the network and considered a "secondary extinction". A network's robustness to extinction was measured as the number of primary (insect) species

extinctions required to cause a loss of 50% of the total species in the network (Dunne et al. 2002). Robustness values range from a maximum of 0.5, where primary extinctions result in no secondary extinctions, to a minimum of 1/S, where S is the number of species in the network.

We calculated robustness values for two types of extinction simulation. First, we conducted deterministic simulations in which insect species were removed in order of abundance, starting with the least abundant species. This extinction order was used because it has frequently been shown that rare, specialist-foraging pollinators are often at particular risk of decline (Memmott et al. 2004, Biesmeijer et al. 2006, Bartomeus et al. 2013). However, because it can be difficult to predict which species may be most vulnerable in highly modified landscapes facing multiple anthropogenic threats, we also conducted simulations in which insect species were randomly removed from networks. Mean robustness values were calculated based on 1000 random removal simulations. Linear models were used to compare robustness values between remnant and reconstructed sites, for each of the two types of simulation.

Finally, we evaluated whether plant and animal species shared among remnant and reconstructed prairies tended to exhibit similar species-level interaction specialization at each type of site. These analyses were restricted to consider only species that were recorded in plant-pollinator networks in at least three remnant- and three reconstructed prairies. We calculated the interaction specialization for each species at each site using *d'*, an index of specialization related to H_2' that takes into account a focal species' proportional utilization of its partners as well as the partners' proportional availability (Blüthgen et al. 2006). Values of *d'* range from 0 to 1, with higher values indicating greater interaction specialization. Mean *d'* values were calculated for each species for remnant sites and reconstructed sites, respectively. We then performed separate correlation tests for flower visitor and forb species to assess whether there was a positive

correlation between *d'* values across remnant and reconstructed prairies. A one-tailed Pearson's correlation test was performed for the shared forb species. Because the flower visitor data were not normally distributed, we generated *P*-values for these data from a Spearman's correlation test.

Results

Overview

From 2013-2015 we recorded 6679 interactions between forbs and flower visiting insects during 99 total surveys (Fig S3.1-S3.10 in Appendix 3). The resulting networks encompassed 326 insect taxa (85% of individuals were resolved to species; 97% resolved to genus or finer) visiting 96 forb taxa (89% of which were resolved to species; 97% resolved to genus level or finer). Coleoptera, Hymenoptera, Diptera and Lepidoptera were the four most abundant insect orders recorded, representing 33%, 33%, 15% and 14% of individuals (95% of total insects), respectively. The most abundant plant families recorded were Fabaceae and Asteraceae, representing 64% and 29% of the floral abundance recorded (93% of total floral abundance). The ten most abundant forb and flower visitor species are listed in Tables 3.1 and 3.2. Remnant sites were sampled a total of 50 times (mean $\pm$ 1 S.E. = 10 $\pm$ 0.45) and reconstructed sites were sampled a total of 49 times (mean $\pm$ 1 S.E. = 9.8 $\pm$ 0.37). There was no significant difference in sampling effort between remnant and reconstructed prairies, based on the number of times the site types were sampled ($t = 0.34$, $P = 0.740$). Therefore, we did not include a sampling effort term in subsequent statistical models.

Network Properties

Overall, plant-pollinator networks on reconstructed prairies were structurally similar to those of prairie remnants. There was no significant difference in network size between remnants

and reconstructed prairies regardless of whether they were measured additively ($t = 0.12$, $P = 0.910$; Fig. 3.1A) or multiplicatively ($t = 0.84$, $P = 0.426$; Fig. 3.1B). Remnant and reconstructed plant-pollinator networks did not differ significantly in network-level specialization (H_2': $t = -0.19$, $P = 0.855$; Fig. 3.1C), nestedness (WNODF: $t = -0.60$, $P = 0.566$; Fig. 3.1D), or modularity (Q^{norm}: $t = 0.23$, $P = 0.825$, Fig. 3.1E). Our null models indicated that all networks were structured by significant network-level specialization ($P < 0.001$ for all networks), and that all networks were significantly non-nested ($P < 0.001$ for all networks) and significantly modular ($P < 0.001$ for all networks). The species composition of modules was largely variable across sites. However, two notable trends were evident. First, six of the ten networks contained a module that was characterized by two closely related members of the Asteraceae family (Urbatsch et al. 2000) that were frequently recorded across the study sites— *Rudbeckia hirta* and *Ratibida pinnata*— and a set of generalist flower visitors that were often frequently recorded, including *Typocerus confluens* and *T. octonotatus* (Coleoptera: Cerambycidae), *Phyciodes tharos* (Lepidoptera: Nymphalidae), and *Halictus ligatus* (Hymenoptera: Halictidae). Second, when specialist foragers (e.g. oligolectic bees) were recorded at a site, they were very frequently, and not surprisingly, found in the same module as their known host plants. For example, the pollen specialist bees *Andrena helianthiformis* and *Andrena rudbeckiae* (Andrenidae) were almost always found in the same module as their respective host genera, *Echinacea* (Asteraceae) and *Rudbeckia/Ratibida*, respectively.

Plant-pollinator networks on remnant and reconstructed prairies displayed very high levels of robustness to insect species loss both when insects were removed from least- to most abundant and when insects were removed randomly. Robustness did not differ between the two site types under either the deterministic removal scenario ($t = 0.541$, $P = 0.603$; Fig. 3.1F) or the

random removal scenario (t = -0.78, P = 0.460; Fig. 3.1F). Under the deterministic removal scenario, secondary (forb species) extinctions accumulated very slowly as flower visitor species were removed from the networks, only accelerating towards the end of each simulation (Fig. S3.11A). The pattern of secondary extinctions was similar under the random removal scenario, although it more closely approximated a linear relationship (Fig. S3.11B).

Of the 96 forb taxa recorded during the field surveys, 11 species were recorded on at least three remnant and reconstructed prairies, representing 11% of the total forb species recorded across the sites, and 53% of the total forb abundance recorded. Thirty-nine of the 326 insect taxa we recorded were found on at least three of each site type, representing 12% of the total insect species and 72% of the total insect individuals recorded across all sites. Forb species that were shared among sites were not significantly correlated in their niche breadth (Pearson's r = 0.39, t = 1.29, P = 0.115; Fig. 3.2A). However, this lack of correlation was driven by one species, *Asclepias syriaca* (Asclepiadaceae). *A. syriaca* had a high mean specialization value on prairie remnants (mean $\pm$ 1 S.E. = 0.80 $\pm$ 0.083) but was only moderately specialized (d' = 0.53 $\pm$ 0.11) on reconstructed prairies. When this species was removed from the analyses, the correlation became strongly positive and statistically significant (Pearson's r = 0.78, t = 3.52, P = 0.00390), indicating that niche breadth for shared forbs was, for the most part, similar across remnant and reconstructed prairies. For shared flower visitor species, we found a significant, positive correlation between niche breadth on prairie remnants and reconstructed prairies (Spearman's ρ = 0.28; P = 0.0449; Fig. 3.2B).

Discussion

In recent years, the science of restoration ecology has shifted to incorporate functional, as well as structural, endpoints (Devoto et al. 2012). A network approach is valuable in that it

allows researchers to evaluate the effects of restoration on the complex patterns of species interactions mediating key ecological functions (Schleuning et al. 2015). Although we previously uncovered substantial differences between remnant and reconstructed prairies' forb communities (Denning and Foster 2018; dissertation Chapter 1), herein we show that these differences did not extend to network structural properties, which were similar across both types of prairie. Networks were modular, specialized and robust to species removal, with shared taxa exhibiting similar niche breadths across remnant and reconstructed prairies. Taken together, this suggests that habitat restoration has successfully reinstated functioning plant-pollinator networks in this system.

Network-Level Metrics

The challenges of reinstating forb biodiversity during prairie restoration are well-documented (Kindscher and Tieszen 1998). Indeed, our previous work demonstrated that forb diversity was lower on reconstructed prairies (Denning and Foster 2018; dissertation Chapter 1), suggesting that plant-pollinator networks, in turn, could be relatively species-poor and could thus differ fundamentally in network structure, compared to remnant prairies' networks. Nevertheless, we found no significant differences in network size between the two types of prairie.

We also failed to find differences in nestedness between remnant and reconstructed prairies, as networks were consistently non-nested and modular. This contrasts a wealth of previous work indicating that mutualistic networks are highly nested (reviewed in Bascompte and Jordano 2007). However, nestedness analysis is sensitive to the choice of both nestedness metric and null model (Ulrich et al. 2009). Our study utilized WNODF (Almeida-Neto and Ulrich 2011), a metric incorporating species abundances. It is possible for networks to differ in nestedness depending on whether abundance data are included. For example, Staniczenko et al

(2013) evaluated nestedness across 52 networks and found that whereas networks consisting of species presence-absence data were often nested, weighted networks (i.e. those incorporating species abundances) were largely non-nested. Recent studies from multiple ecosystems have also found low nestedness values across weighted networks. Traveset et al. (2016) recorded a relatively low mean WNODF value ($\bar{x} = 13.32$) across 52 mainland and island networks. Networks from tropical savannahs (Moriera et al. 2015) and montane meadows (Olito and Fox 2015) yielded WNODF values strikingly similar to ours ($\bar{x} = 9.02$ and 9.59, respectively, versus $\bar{x} = 9.23$ at our sites). The similarity of these values supports the hypothesis that there are common ecological mechanisms underpinning network buildup and stability across diverse ecosystems (Bascompte and Jordano 2007).

We also used a conservative null model in which row and column totals, representing visitation frequency and the abundances of each flower visitor species, respectively, were fixed. This approach was chosen because we believe that, in our system, allowing these factors to be unconstrained is biologically unrealistic. This builds on the work of Ulrich et al. (2009), who used fixed row and column null models to reassess the nestedness of a set of species distribution matrices, finding that few of these matrices were nested under this conservative null model approach. Taken together, these studies indicate that nestedness may not be as pervasive across plant-pollinator networks as was previously thought.

In nested networks, specialist species interact with subsets of the species that generalists interact with, leading to substantial interaction redundancy. In contrast, low nestedness indicates that species interactions are partitioned. Two additional network properties we observed— modularity and network-level specialization— further support the interpretation that interaction partitioning is a consistent feature of networks in our system. Networks across remnant and

reconstructed prairies were significantly modular, consisting of multiple subsets (modules) of species that interacted more frequently with one another than with members of other modules. Network modularity can reflect multiple evolutionary and ecological processes that constrain species' interactions, including phenology, spatial heterogeneity in the availability of interaction partners, and patterns of coevolution and trait convergence (Pimm and Lawton 1980, Lewinsohn et al. 2006, Martín González et al. 2012, Dupont et al. 2014, Tur et al. 2015).

The modular structure of the networks in our study likely stems from many of the above, non-mutually exclusive, processes. For example, the abundant composites *Rudbeckia hirta* and *Ratibida pinnata* have long, overlapping flowering periods and shallow florets, which are likely accessible to a wide range of flower visiting insects. Therefore, the composition of the *R. hirta*-*R. pinnata* module recorded across several sites is probably partially reflective of overlapping phenologies, with generalist insects foraging opportunistically on abundant, easily accessible flowers. However, given that some modules in this study, including the *R. hirta*-*R. pinnata* module, were also characterized by specialist foragers (e.g. *Andrena helianthiformis* and *A. rudbeckiae*; Neff and Simpson 1997, Arduser 2014) and their host plants, it is likely that a suite of ecological and evolutionary factors that govern specialization (e.g. competition avoidance, morphological and neurological constraints; Futuyma and Moreno 1988, Michener 2007) also structure these modules.

Because network-level specialization can be interpreted as the degree of niche partitioning in a network (Blüthgen et al. 2006), the significant specialization we observed provides additional evidence that interaction partitioning is a key feature of the networks in our system, and that interactions are not governed solely by species abundances. We predicted that lower forb diversity on reconstructed prairies could lead to smaller, less complex, and therefore,

less specialized networks, but this expectation was not borne out. Interestingly, our results mirror those of Fründ et al. (2010), who demonstrated that plant-pollinator networks in German meadows were moderately specialized ($\bar{x} = 0.51$, similar to our overall mean of 0.53) and that specialization did not vary across a gradient in forb diversity. In their system, specialization was driven by flower visitor species that are typically thought of as generalists but were found to display distinct foraging preferences across their sites (Fründ et al. 2010). Collecting foraging breadth information from the literature for the hundreds of insect taxa we recorded was beyond the scope of this study. However, we did collect this information for bees, the primary pollinators worldwide and a well-represented group in our study. Despite significant network-level specialization, the great majority of bee species and individuals we recorded are considered generalist foragers (K.R.D., unpublished data). This highlights the need for future studies in the tallgrass prairie that examine the extent to which species that are typically considered generalists exhibit local specialization, potentially for different forb species across different sites.

Species-Level Metrics

Most previous studies on the effects of ecological degradation and restoration on plant-pollinator networks have focused on network-level structural properties (e.g. nestedness, connectance; Soares et al. 2017). However, many network-level properties are highly conserved across a wide array of ecosystems (Bascompte and Jordano 2014), and network-level properties that are robust to perturbations could mask substantial species-level changes within networks (Nielsen and Totland 2014). In their recent meta-analysis, Soares et al. (2017) found that, unlike several network-level properties, species-level specialization (*d'*) consistently responded to environmental degradation. In contrast, we found that both network-level properties (e.g. network size, nestedness, modularity) and *d'* were largely consistent between remnant and

reconstructed prairies. In other words, forb and flower visitor species that were generalists/specialists on prairie remnants tended to exhibit a similar niche breadth on reconstructed prairies. The shared species comprised over half of the total forb and insect abundances recorded across the sites, suggesting that the similarities in network-level properties between remnant and reconstructed prairies may be mediated by the consistency in niche breadth among these abundant shared species.

Network Functioning and Implications for Ecological Restoration

One major opportunity in the ever-growing field of network biology involves linking network properties to the functioning and stability of communities facing multiple anthropogenic pressures. As such, the primary goal of this study was to compare network architecture across remnant and reconstructed prairies to infer whether habitat restoration can reinstate plant-pollinator interactions. Two lines of evidence suggest that restoration has been successful in this system. First, regardless of the specific architectural features of these networks, the striking similarity in network architecture between reconstructed and remnant prairies suggests that habitat restoration has indeed reinstated important aspects of these plant-pollinator networks. Second, modularity and network-level specialization, which were pervasive features of the networks in this study, may play important roles in contributing to network stability and species coexistence, respectively. Disturbances may spread more slowly through modular networks, potentially fostering network stability by containing perturbations within individual modules, thus minimizing the effects on other modules (Krause et al. 2003, Olesen et al. 2007). Network-level specialization indicates that these communities exhibit substantial niche partitioning, which may, in turn, facilitate species coexistence by decreasing interspecific competition (Blüthgen and Klein 2011). However, these interpretations are each subject to important caveats. While the

similarity in network properties between remnant and reconstructed prairies may signify restoration success, it is important to note that the prairies in our study are embedded in agricultural landscapes that have been heavily modified by human activities. Our previous work in this system (Denning and Foster, *in press*, Biological Conservation; dissertation Chapter 2) indicates that the composition and configuration of these surrounding landscapes may be important drivers of flower visitor community structure. Therefore, a reasonable alternative interpretation is that networks across both remnant and reconstructed prairies exist in a similarly degraded state, and that small, isolated prairie remnants may not be appropriate reference sites to gauge restoration success. In addition, it can be difficult to use measures such as specialization and modularity to draw clear inferences about the status and stability of complex ecological functions. Indeed, within the framework of habitat restoration in highly modified landscapes, a modular network structure could be seen as unfavorable, as the loss of "connector" species that link modules could fundamentally alter network structure (Bascompte and Jordano 2014). Moreover, whereas the interaction partitioning that accompanies network-level specialization may promote coexistence and biodiversity, a reduction in network-level specialization has also been interpreted as a successful restoration outcome, as the interaction redundancy in more generalized networks could promote network stability (Kaiser-Bunbury et al. 2017). While we are not able to disprove these alternative interpretations, the robustness to simulated species loss that our networks exhibited provides a particularly compelling line of evidence that habitat restoration has been successful. In both removal scenarios, initial losses of flower visitor species resulted in only gradual forb species losses, with forbs exhibiting a rapid decline only after a large proportion of the flower visitor species were removed. This was especially evident in the deterministic scenario, where species were removed from least- to most abundant. This result is

similar to that of that of other studies utilizing extinction simulations to measure network robustness (e.g. Memmott et al. 2004, Kaiser-Bunbury et al. 2010). Several architectural features of plant-pollinator networks may contribute to their robustness. For example, plant-pollinator networks, including those in this study, often exhibit interaction distributions where a small number of species have many interaction partners, and a large number of species are characterized by few interaction partners (Bascompte and Jordano 2007). This structure, which often follows a truncated power-law distribution, allows networks to withstand the loss of less-connected or randomly chosen species without suffering immediate collapse (Memmott et al. 2004). Furthermore, the interaction redundancy and asymmetry that characterize nested networks may be particularly important for imparting robustness (Memmott et al. 2004). Nevertheless, our work indicates that even non-nested, modular networks can be highly robust to species loss.

Conclusions

Ecosystems are fundamentally structured by biotic interactions, with interactions between plants and pollinators resulting in the provisioning of a key ecological service. However, few studies have evaluated the responses of plant-pollinator networks to ecological restoration (Kaiser-Bunbury and Blüthgen 2015), likely because of the many challenges inherent in studying these diverse, complex communities. Given that plant-pollinator networks across both remnant and reconstructed prairies displayed similar architecture and were robust to species loss, our work suggests that functioning flower visitor communities have been successfully restored in this system. One important caveat of this interpretation is that our study, like the vast majority of plant-pollinator network studies, used observational data of insects visiting flowers without assessing whether pollen transfer was occurring. Our future work will evaluate pollen transport among tallgrass prairie bees, to assess whether network properties, and thus, interpretations

regarding restoration success, remain consistent using this approach. Ultimately, our study adds to the small, but growing body of research indicating that a network approach can provide valuable information about restoration success to researchers and practitioners.

Figures and Tables

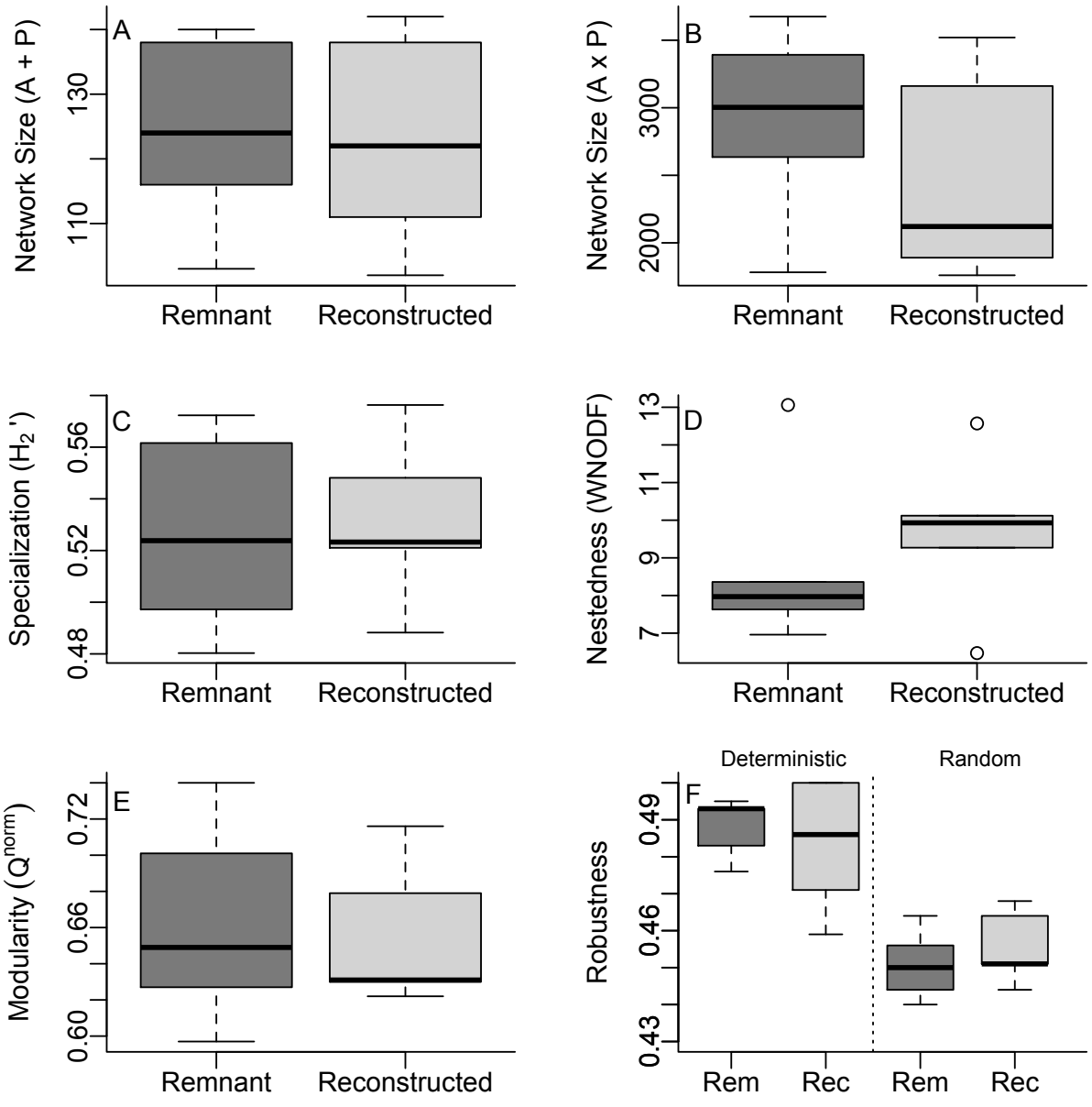

Figure 3.1. Comparison of plant-pollinator network structure between remnant and reconstructed tallgrass prairies sampled from 2013-2015 in northeast Kansas. **A)** Network size, measured as the combined number of animal (A) and plant (P) species; **B)** Network size, measured multiplicatively; **C)** Network-level specialization (H_2'); **D)** Network nestedness (WNODF); **E)** Network modularity; **F)** Robustness of networks to species extinctions, when insect species were removed from the networks from least to most abundant (left), and when insect species were removed randomly (right; averaged over 1000 simulations).

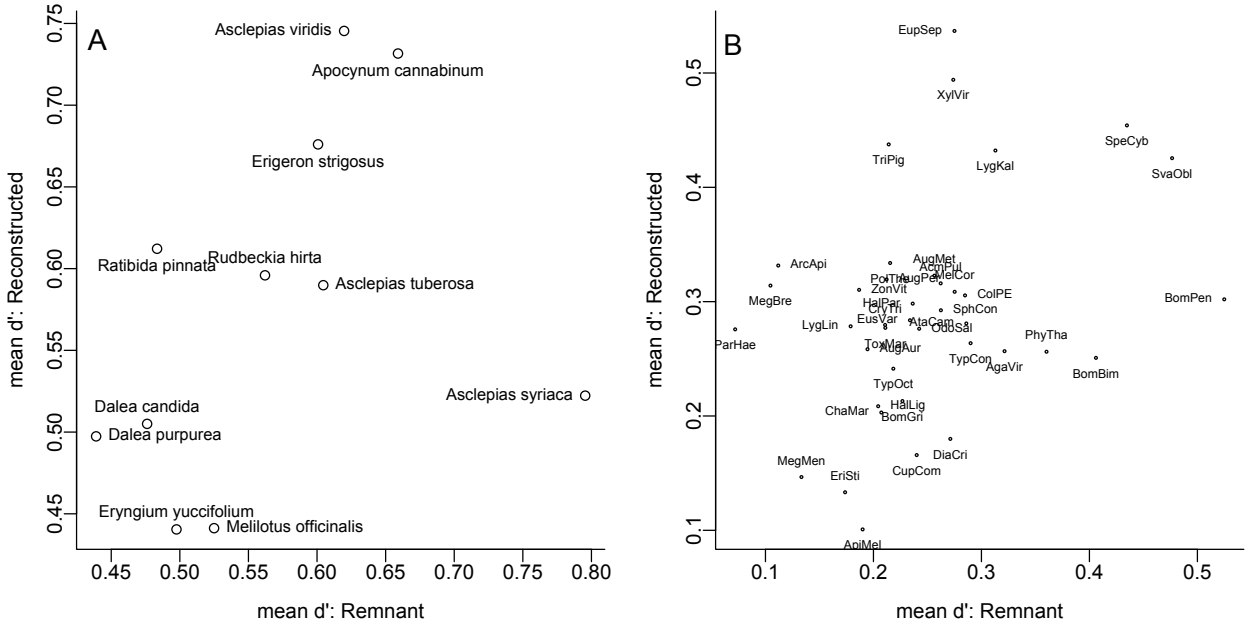

Figure 3.2. Niche breadth (*d'*) comparisons on prairie remnants and reconstructed prairies for **A)** 11 shared forb species. Forb species were not significantly correlated (Pearson's r = 0.39, t = 1.29, P = 0.115) unless *A. syriaca* was removed (Pearson's r = 0.78, t = 3.52, P = 0.00390); **B)** Thirty-nine shared flower visitor species. Insect species were significantly positively correlated in their niche breadths across the two site types (Spearman's ρ = 0.28; P = 0.0449). Insects are abbreviated using the first three letters of the genus and specific epithet. Coleoptera: *Acmaeodera pulchella*, *Chauliognathus marginatus*, *Cryptorhopalum triste*, *Diabrotica cristata*, *Euphoria sepulcralis*, *Odontocorynus salebrosus*, *Trichiotinus piger*, *Typocerus confluens*, *Typocerus octonotatus*, *Zonitis vittigera*; Diptera: *Archytas apicifer*, *Eristalis stipator*, *Paragus haemorrhous*, *Sphaerophoria contigua*, *Toxomerus marginatus*; Hemiptera: *Euschistus variolarius*, *Lygus kalmii*, *Lygus lineolaris*; Hymenoptera: *Agapostemon virescens*, *Apis mellifera*, *Augochlorella aurata*, *Augochlorella persimilis*, *Augochloropsis metallica*, *Bombus bimaculatus*, *Bombus griseocollis*, *Bombus pensylvanicus*, *Halictus ligatus*, *Halictus parallelus*, *Megachile brevis*, *Megachile mendica*, *Megachile coreopsis*, *Svastra obliqua*, *Xylocopa virginica*; Lepidoptera: *Atalopedes campestris*, *Colias phylodice/eurytheme*, *Cupido comyntas*, *Phyciodes tharos*, *Polites themistocles*, *Speyeria cybele*

Table 3.1. The 10 most abundant forb species recorded across 10 tallgrass prairie sites in northeast Kansas from 2013-2015. Abundance was measured as the total size of the floral display, added across all sites and years.

Rank Abundance	*Species* (Family)	Total Size of Floral Display (cm^2)
1	*Melilotus officinalis* (Fabaceae)	107049
2	*Trifolium campestre* (Fabaceae)	99239
3	*Rudbeckia hirta* (Asteraceae)	86765
4	*Erigeron strigosus* (Asteraceae)	31234
5	*Melilotus alba* (Fabaceae)	30170
6	*Trifolium pratense* (Fabaceae)	28465
7	*Psoralidium tenuiflorum* (Fabaceae)	13942
8	*Dalea purpurea* (Fabaceae)	9873
9	*Penstemon digitalis* (Scrophulariaceae)	6574
10	*Dianthus armeria* (Caryophyllaceae)	4733

Table 3.2. The 10 most abundant flower visitor species recorded across 10 tallgrass prairie sites in northeast Kansas from 2013-2015. Abundance was measured as the total number of individuals recorded across all sites and years.

Rank Abundance	*Species* (Order: Family)	Number of Individuals
1	*Diabrotica cristata* (Coleoptera: Chrysomelidae)	686
2	*Toxomerus marginatus* (Coleoptera: Cerambycidae)	496
3	*Apis mellifera* (Hymenoptera: Apidae)	454
4	*Cryptorhopalum triste* (Coleoptera: dermestidae)	384
5	*Typocerus octonotatus* (Coleoptera: Cerambycidae)	359
6	*Augochlorella aurata* (Hymenoptera: Halictidae)	244
7	*Chauliognathus marginatus* (Coleoptera: Cantharidae)	234
8	*Bombus griseocollis* (Hymenoptera: Apidae)	223
9	*Cupido comyntas* (Lepidoptera: Lycaenidae)	210
10	*Typocerus spp.* (Coleoptera: Cerambycidae)	198

General Discussion

Overview

The processes governing the assembly of ecological communities occur over a wide range of spatial and temporal scales, and developing our understanding of these processes is critical both to advancing ecological theory and conserving Earth's biodiversity. In this dissertation, I used the context of tallgrass prairie habitat reconstruction to investigate potential drivers of flower visitor community structure and plant-pollinator network architecture. In Chapter 1, I compared forb and insect flower visitor abundance, diversity and species composition across remnant prairies and prairies reconstructed on former croplands in northeast Kansas. Whereas forb communities exhibited substantial differences, flower visitor communities were largely comparable between the two types of prairie. In Chapter 2, I examined potential site- and landscape scale drivers of flower visitor community structure, finding that flower visitor α-diversity was generally not strongly associated with site-scale forb α-diversity (with the notable exception of bees), but instead exhibited taxon-specific associations with the composition and configuration of the landscapes surrounding the sites. In Chapter 3, I returned to a direct comparison of remnant and reconstructed prairies, evaluating whether the architecture and robustness of plant-pollinator networks was reinstated via prairie reconstruction. I found that plant-pollinator networks were highly similar in structure between prairie remnants and reconstructed prairies, and that networks were robust to simulated species removal.

Overarching Conclusions

Two general conclusions can be drawn from these studies. First, these results suggest, though do not conclusively demonstrate (see caveats below), that the reconstruction of prairies on former croplands can successfully reinstate insect pollinator communities. The well-known

challenges of reinstating forb diversity during prairie reconstruction led me to predict (Chapter 1) that lower forb diversity on reconstructed prairies would likely lead to suppressed flower visitor diversity, given that both floral resources (pollen, nectar) and plant resources more broadly (e.g. nesting materials such as pithy stems, leaves) are critical for pollinators. Nevertheless, flower visitor diversity, abundance and composition were largely similar when compared between remnant and reconstructed prairies. This result extended to plant-pollinator networks as well. Network structure was remarkably similar between remnant and reconstructed prairies, and the particular features of these networks (e.g. high modularity, low nestedness, robustness to species loss) are thought to confer network stability and promote species coexistence, lending further evidence to the interpretation that prairie reconstruction has been successful.

Second, my findings indicate that key aspects of flower visitor community structure in this system appear to be more strongly driven by landscape context than by site-scale forb communities. This finding may be especially relevant for researchers investigating how community assembly is governed across a wide range of spatial scales. The legacy of previous land use (e.g. intensive farming that the prairie reconstruction sites were subjected to) is known to have long-lasting effects on many aspects of ecosystem structure and function, including soil chemistry, plant composition, and vulnerability to stress and disturbance (Foster et al. 2003). Moreover, the role of fine-scale processes and interactions (e.g. resource competition, trophic interactions) in governing community assembly has been well established, and many previous studies have demonstrated that flower visitor diversity can be strongly associated with forb diversity at the scale of focal sites (Potts et al. 2003, Kennedy et al. 2013). Nevertheless, I found that flower visitors (except for bees, considered independently) were not strongly associated with site-scale forb α-diversity. Instead, flower visitors frequently exhibited taxon-specific

associations with the composition and configuration of the surrounding landscapes. In addition, despite a history of agricultural conversion, plant-pollinator networks on prairie reconstructions (and those on prairie remnants) were highly robust to perturbation in the form of simulated species loss.

In this study system, remnant and reconstructed prairies were situated within landscapes that were largely similar in the proportion and edge density of both warm-season grasslands and natural/semi-natural lands (K.R. Denning, unpublished data). Therefore, the similarities in pollinator community structure between remnant and reconstructed prairies may be in large part attributable to the consistency of landscape context. This interpretation makes intuitive sense, given the well-documented mobility of flower visiting insects and the relatively small size of the tallgrass prairie sites used for this study.

It is important to point out that despite few links between forb and flower visitor α-diversity, site-scale forb communities were not inconsequential in structuring flower visitor communities. Rather, it appears that forb composition at the scale of these focal prairies may be strongly influencing the composition of flower visitors found at these sites. Because we recorded insects while they were visiting flowers, it is likely that this concordance resulted from trophic interactions between flower visitors and forbs, and several of the flower visitor taxa we observed are indeed specialist feeders on particular plant families as either larvae or adults. The significant concordance in community composition may also have been caused by both forbs and insects responding similarly to ecological patterns or processes that we did not measure. For example, some bee species require specific soil substrates for nesting, and these abiotic conditions are also associated with distinctive plant assemblages.

Applications and Future Research

For practitioners and policy makers, these findings highlight the importance of practicing conservation and ecological restoration at the landscape scale, especially when the focus of these efforts centers around highly mobile organisms such as insect pollinators. While still extensive, tallgrass prairie losses in Kansas are lower than in many other U.S. states (Samson and Knopf 1994). Therefore, given the importance of landscape context in this system, it may be the case that if this study had been conducted in landscapes experiencing much more degradation and fragmentation (e.g. the intensively farmed landscapes of Iowa or Illinois, where >99% of the historic tallgrass prairie has been lost; Samson and Knopf 1994), I would not have observed a corresponding "recovery" of a diverse flower visitor community. More work across a wider gradient of landscape degradation is needed to determine whether this would be the case.

In addition, these results indicate that practitioners working in the highly-fragmented tallgrass prairie ecosystem should use an abundance of caution when using forb α-diversity at a focal site to make predictions about flower visitor α-diversity. Practitioners should not expect that more forb-diverse tallgrass prairie sites will necessarily also be more pollinator diverse. However, because I found significant concordance between forb and flower visitor composition, practitioners may be able to accurately utilize forb composition data (which are often much easier to obtain than insect data) to make predictions about the likely flower visitor species present at a focal site. This may be particularly useful for practitioners with limited access to insect taxonomic expertise.

For researchers focused on developing ecological theory, these findings may lead to several fruitful avenues for future work, particularly as it relates to the assembly of the mutualistic interactions that comprise plant-pollinator networks. Two lines of inquiry that I find especially interesting are highlighted as follows: First, given the apparent importance of

landscape composition and configuration in governing the assembly of flower visitor communities in this system, a logical extension of this work would be to explicitly evaluate the effects of landscape context on the interactions that underlie the architecture of plant-pollinator networks. Despite the prevalence of anthropogenic habitat loss and degradation, very few studies have examined the effects of habitat fragmentation on plant-pollinator network structure (Astegiano et al. 2015). The tallgrass prairie ecosystem may be especially useful for this type of work, as a natural gradient of prairie fragmentation can be found from relatively intact tallgrass prairies characterizing the Kansas Flint Hills to incredibly small, isolated remnant prairie habitats situated in the intensively managed agricultural landscapes of several Midwestern states (Samson and Knopf 1994). Second, the findings outlined in Chapter 3 naturally raise the question of whether network structure among remnant and reconstructed prairies would remain similar when other types of interactions are integrated into these networks. Our understanding of networks that comprise a single type of interaction (e.g. pollination, seed dispersal) has increased greatly over the last two decades. However, with few exceptions (e.g. May 1972), ecologists have only very recently initiated theoretical and empirical investigations of networks comprising multiple types of biotic interactions (Garcia-Callejas et al. 2018). One pervasive type of interaction that has received relatively little attention in network studies is that of plants and root-associated fungi. Interestingly, recent work from Toju et al. (2015) found that plant-fungal networks can be highly non-nested and modular; architectural features that mirror that of the plant-pollinator networks in this study. Among myriad possibilities, future work in this system could examine, in "multi-layer" networks, (1) whether plant-pollinator sub-network structure mirrors that of plant-fungal sub-networks. For example, are plants that act as module hubs for pollinators playing the same role for fungal associates? If so, how would that affect network stability and species

coexistence?; (2) the potential mechanisms by which one type of ecological interaction affects another. For example, do plant-fungal associations alter plant biomass allocation, thereby influencing plants' interactions with pollinators? How might that affect the assembly of complex networks in the context of ecological restoration?

Limitations of this Research

Two important caveats regarding the studies in this dissertation should be noted. The first involves the use herein of relatively small, isolated prairie remnants as references against which to evaluate restoration success. In their 2004 *Primer on Ecological Restoration*, the Society for Ecological Restoration (SER) outlined nine key attributes of restored ecosystems. The very first attribute states, in part, that "the restored ecosystem contains a characteristic assemblage of the species that occur in the reference ecosystem". The reference site serves as a benchmark of ecosystem health against which the success of ecological restoration is measured. In the studies comprising this dissertation, I chose as reference sites small, often isolated remnant prairies that were located relatively close to the reconstructed prairies I was evaluating. These sites were embedded in landscapes that contained a substantial proportion of intensively managed lands, and, as I demonstrated in Chapter 2, landscape context can be highly influential in structuring flower visitor communities. Therefore, it is possible that the similarity in flower visitor community structure and plant-pollinator network architecture that I observed is not indicative of restoration success, but instead demonstrates that flower visitor communities across both remnant and reconstructed prairies exist in a similar state of human-mediated degradation. Unfortunately, given the extent of the destruction of the tallgrass prairie, large tracts of remnant tallgrass prairie that would have made more suitable reference sites are incredibly uncommon. One such expanse, the Flint Hills of eastern Kansas, would likely have made a more appropriate

reference against which to evaluate these reconstructed prairies. However, due to the time-intensive nature of the pollinator surveys I conducted, using Flint Hills prairies as a reference was not feasible.

Despite this caveat, two lines of evidence—the presence of specialist species and the robustness of plant-pollinator networks—suggest that the observed similarities between remnant and reconstructed prairies are indeed indicative of restoration success. Because diet- and habitat specialist pollinators are particularly susceptible to ecological degradation (Biesmeijer et al. 2006, Bartomeus et al. 2013), it is likely that degraded sites would have few such species. However, as I noted in Chapter 1, both remnant and reconstructed prairies were found to have numerous specialists, including cleptoparasitic bee species, a life history strategy deemed particularly vulnerable to disturbance (Sheffield et al. 2013). Second, as I outlined in Chapter 3, the robustness of plant-pollinator networks across all of the sites to simulated species loss lends further weight to the interpretation that habitat reconstruction has been successful.

The second major caveat is that despite this dissertation's emphasis on pollination and pollinator declines, I did not assess the rates or efficacy of pollen transfer in this system, instead basing my sampling strategy on visual observations. Although this approach is very common, it is also problematic, as insects are found on flowers for a variety of reasons, and not all visits lead to pollination. During my surveys, I attempted to minimize this problem by only recording insects observed to be in contact with floral reproductive structures. In addition, I am currently working on a project complementary to this dissertation, wherein I will use a high-throughput sequencing approach to evaluate pollen transfer by a subset of the bees recorded during these prairie surveys. By comparing the architecture of these pollen transport networks to that of the

observation based networks, I will be able to more fully evaluate the restoration of pollination services in this system.

Conclusion

As humans continue to exert pressure on Earth's ecosystems, it becomes increasingly important to develop our understanding of the multi-scale drivers of flower visitor community structure, not only to develop ecological theory but also to ensure that these communities can be adequately conserved or restored. This dissertation research indicates that (1) the apparent effects of land use legacies and ecological restoration practices on forb community assembly do not extend to flower visitor communities, but that (2) landscape context likely plays a crucial role in structuring flower visitor communities and that (3) current ecological restoration practices in tallgrass prairies may be effective for reinstating flower visitor community structure and plant-pollinator interactions. It is my hope that this dissertation research will be particularly valuable for informing ecological restoration plans in the tallgrass prairies and for stimulating future research in the ever-expanding fields of community assembly and network biology.

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Appendix 1: Supplemental Figures and Tables for Chapter 1

Table S1.1. Site characteristics and sampling effort for each of 10 prairie study sites in northeast Kansas. CRP = Conservation Reserve Program; REC = reconstructed prairie, REM= remnant prairie. Sites were chosen by soliciting volunteers via the Kansas Native Plant Society and the Kansas Biological Survey. The shape of the sites varied, following the topography of the area. Sampling effort represents the number of site visits in each of the three respective study years.

Site	Coordinates (°N;°W) : KS County	Type	Size (ha)	Reconstruction and Management History	Sampling Effort
Anderson Family (AND)	39.458; 95.513 Atchison	REM	5.8	Hayed annually	4, 4, 3
Baker Farm (BAK)	39.189; 95.610 Shawnee	REC	3.1	Seeded with 6 grasses and several forbs in 2007. Fifteen additional forb species added in 2013. Burned and hayed periodically.	4, 3, 3
Busby (BUS)	38.830; 95.141 Douglas	REC	5.2	Enrolled in CRP in 1999.Ten grasses and 121 forb species introduced across all CRP fields (including the study site) from 2001-2003. Burned approximately every 3 years. Mowing and spot-spraying of noxious weeds.	4, 4, 3
Byers Family (BYE)	39.741; 95.285 Doniphan	REC	3.5	Enrolled in CRP in 2008, and seeded with six native grasses and 41 forb species. Burned approximately every 3 years.	3, 4, 3
Coombs (COO)	39.451; 95.614 Jackson	REC	5.2	Drilled with 12 native grasses and 36 forbs in 2009. Periodically burned and hayed. Spot spraying for noxious weeds.	4, 3, 2
Guess (GUE)	38.984; 95.405 Douglas	REM	4.4	Hayed annually. Burned every 3-5 years.	3, 4, 3

Site	Coordinates (°N;°W) : KS County	Type	Size (ha)	Reconstruction and Management History	Sampling Effort
Kettle-Look (KET)	38.886; 95.385 Douglas	REC	7.0	In 1992, 6 grass species and two forb mixes (total number unknown) were drilled in. Hayed annually.	3, 3, 3
Rockefeller (ROC)	39.045; 95.205 Jefferson	REM	3.5	Hayed until 1957. Burned every 1-3 years from 1957-2006. Burned and/or hayed approximately every 1-3 years since 2007.	3, 3, 3
Snyder (SNY)	39.326; 95.660 Jackson	REM	5.7	Burned approximately every 2-3 years. Mowing and spot-spraying as needed to reduce woody cover.	3, 3, 3
Teal Lake (TEA)	38.868; 95.646 Osage	REM	3.8	Burned or hayed approximately every 1-2 years.	4, 4, 3

Table S1.2. Flower visitor abundance data collected from five remnant- and five reconstructed prairies in Kansas from 2013-2015. Only taxa that were identified to genus- or species-level resolution are included in this table. A = oligolectic bees (*i.e.* bees that collect pollen from specific plant families, genera or species; Arduser 2014); B = cleptoparasitic bees; C = butterflies that are likely prairie habitat specialists (Reed 1996).

	Remnant			Reconstructed			
	2013	2014	2015	2013	2014	2015	**Total**
Coleoptera							
Buprestidae							
Acmaeodera pulchella	3	3	3	0	2	6	**17**
Acmaeodera tubulus	0	0	1	2	0	0	**3**
Cantharidae							
Belotus abdominalis	0	1	0	0	0	0	**1**
Chauliognathus marginatus	2	110	23	14	45	40	**234**
Carabidae							
Lebia vittata	0	0	1	0	0	0	**1**
Cerambycidae							
Batyle suturalis suturalis	0	0	0	3	2	0	**5**
Tetraopes tetrophthalmus	0	2	0	0	1	0	**3**
Typocerus confluens	12	21	9	20	13	8	**83**
Typocerus octonotatus	53	143	38	48	44	33	**359**
Typocerus sp	72	82	4	27	3	10	**198**
Chrysomelidae							
Anomoea flavokansiensis	1	0	0	1	0	1	**3**
Colaspis sp	0	0	0	0	1	0	**1**
Cryptocephalus calidus	0	0	1	0	0	0	**1**
Diabrotica cristata	326	61	14	158	84	43	**686**
Diabrotica undecimpunctata	4	3	0	0	3	1	**11**
Luperaltica nigripalpis	0	0	0	0	0	3	**3**
Microrhopala vittata	0	0	0	1	0	0	**1**
Myochrous sp	0	1	0	0	0	0	**1**
Pachybrachis sp	1	0	1	1	0	0	**3**
Sennius cruentatus	0	0	1	0	1	1	**3**
Tymnes metasternalis	1	0	0	1	0	0	**2**
Tymnes tricolor	0	1	0	3	1	0	**5**
Coccinellidae							
Coccinella septempunctata	0	1	0	0	0	4	**5**
Coleomegilla maculata	0	0	0	0	0	1	**1**
Cycloneda munda	0	0	0	0	0	1	**1**
Hippodamia convergens	1	0	0	0	0	5	**6**

	Remnant			Reconstructed			
	2013	2014	2015	2013	2014	2015	**Total**
Curculionidae							
Calomycterus setarius	0	0	0	1	0	0	**1**
Centrinites strigicollis	2	9	5	0	0	0	**16**
Epicaerus imbricatus	1	0	1	0	2	0	**4**
Linogeraeus tonsilis	0	0	0	0	0	1	**1**
Merhynchites bicolor	0	1	0	0	0	0	**1**
Odontocorynus salebrosus	22	13	3	39	4	4	**85**
Smicronyx lineolatus	0	0	0	0	2	0	**2**
Stethobaris commixta	0	0	0	1	0	0	**1**
Dermestidae							
Cryptorhopalum triste	64	179	55	25	41	20	**384**
Meloidae							
Epicauta sp	3	4	2	0	7	1	**17**
Nemognatha nemorensis	0	0	0	0	0	2	**2**
Zonitis cribricollis	0	0	0	0	2	0	**2**
Zonitis vittigera	5	4	3	8	3	4	**27**
Ripiphoridae							
Macrosiagon limbata	0	0	1	0	0	0	**1**
Scarabaeidae							
Euphoria sepulcralis	0	2	3	1	1	2	**9**
Popillia japonica	0	0	0	0	1	1	**2**
Strigoderma arbicola	0	0	0	0	2	0	**2**
Trichiotinus piger	1	7	6	2	1	3	**20**
Trigonopeltastes delta	0	1	0	0	0	1	**2**
Diptera							
Bombyliidae							
Bombylius sp	0	0	0	0	1	1	**2**
Exoprosopa meigenii	0	0	1	5	2	0	**8**
Geron sp	8	3	0	4	0	0	**15**
Rhynchanthrax sp	0	1	0	1	0	0	**2**
Systoechus sp	0	0	0	1	0	0	**1**
Villa lateralis	1	1	0	0	0	0	**2**
Villa nigra	0	2	0	0	0	0	**2**
Villa sp	0	0	1	0	0	1	**2**
Conopidae							
Physocephala sagittaria	0	0	0	0	0	2	**2**
Zodion sp	1	0	0	0	0	0	**1**
Dolichopodidae							

	Remnant			Reconstructed			
	2013	2014	2015	2013	2014	2015	**Total**
Neurigona sp	0	0	0	1	0	0	**1**
Milichiidae							
Desmometopa sp	0	0	0	0	1	0	**1**
Muscidae							
Graphomya sp	1	0	0	0	0	0	**1**
Musca sp	0	0	0	0	0	2	**2**
Schoenomyza sp	0	0	0	0	0	1	**1**
Nemestrinidae							
Neorynchocephalis volaticus	0	0	0	2	0	0	**2**
Sepsidae							
Sepsis sp	0	0	0	0	0	1	**1**
Stratiomyidae							
Hedriodiscus binotatus	0	0	0	0	0	1	**1**
Nemotelus sp	0	1	0	0	0	0	**1**
Syrphidae							
Eristalis stipator	12	9	34	9	21	94	**179**
Eristalis transversa	0	0	2	0	4	14	**20**
Eupeodes americanus	0	0	0	1	0	0	**1**
Helophilus fasciatus	0	1	0	0	0	0	**1**
Helophilus latifrons	0	0	2	0	0	0	**2**
Orthonevra nitida	0	0	1	0	0	21	**22**
Paragus haemorrhous	2	2	3	5	1	0	**13**
Sphaerophoria contigua	2	2	11	2	1	23	**41**
Syritta pipiens	1	0	0	0	1	3	**5**
Toxomerus geminatus	0	0	0	0	0	3	**3**
Toxomerus marginatus	16	14	119	63	7	277	**496**
Trichopsomyia sp	0	1	0	0	0	1	**2**
Tachinidae							
Archytas apicifer	4	1	1	8	1	9	**24**
Clausicella sp	0	0	0	0	0	1	**1**
Copecrypta ruficauda	0	0	0	0	1	0	**1**
Cylindromyia sp	0	0	0	1	2	0	**3**
Deopalpus hirsutus	5	1	0	0	5	0	**11**
Distichona sp	1	3	5	0	8	6	**23**
Gonia sp	0	2	0	0	2	0	**4**
Gymnoclytia sp	2	3	2	5	9	6	**27**
Nilea sp	0	1	0	0	1	0	**2**
Onychogonia sp	1	3	1	0	1	0	**6**

	Remnant			Reconstructed			
	2013	2014	2015	2013	2014	2015	**Total**
Paradidyma sp	0	0	0	0	1	0	**1**
Phasia sp	1	1	4	3	1	4	**14**
Prosenoides assimilis	0	0	0	0	0	3	**3**
Tephritidae							
Dioxyna picciola	0	0	0	0	2	0	**2**
Hemiptera							
Berytidae							
Jalysus spinosus	0	0	1	1	1	0	**3**
Cicadellidae							
Paraphlepsius sp	0	1	0	0	0	0	**1**
Coreidae							
Catorhintha mendica	0	0	0	1	0	0	**1**
Merocoris distinctus	0	1	0	0	0	0	**1**
Corimelaenidae							
Corimelaena lateralis	0	2	1	0	0	0	**3**
Galgupha sp	0	1	0	0	0	0	**1**
Cydnidae							
Sehirus cinctus	1	0	0	0	0	0	**1**
Lygaeidae							
Lygaeus kalmii	0	3	0	1	2	0	**6**
Lygaeus turcicus	0	0	0	8	10	0	**18**
Neacoryphus bicrucis	0	1	0	0	0	0	**1**
Neortholomus scolapax	0	0	0	0	1	0	**1**
Oncopeltus fasciatus	0	0	2	0	0	0	**2**
Xyonysius californicus	0	1	0	0	1	0	**2**
Miridae							
Lopidea instabilis	0	0	0	0	1	0	**1**
Lopidea sp	0	0	11	0	0	0	**11**
Lygus lineolaris	3	13	21	9	10	56	**112**
Neurocolpus nubilus	0	0	0	1	0	0	**1**
Polymerus basalis	0	1	2	2	0	0	**5**
Pentatomidae							
Euschistus servus	0	0	1	0	0	0	**1**
Euschistus variolarius	20	19	23	14	14	11	**101**
Thyanta calceata	0	0	0	0	2	0	**2**
Trichopepla semivittata	0	2	0	0	0	0	**2**
Reduviidae							
Apiomerus sp	1	1	0	4	0	0	**6**

	Remnant			Reconstructed			
	2013	2014	2015	2013	2014	2015	**Total**
Sinea incognita	0	0	0	0	1	0	**1**
Rhopalidae							
Harmostes reflexulus	1	0	1	0	1	1	**4**
Jadera haematoloma	0	0	0	0	1	0	**1**
Stictopleurus punctiventris	0	0	0	0	0	1	**1**
Thyreocoridae							
Corimelaena pulicaria	0	0	0	1	0	0	**1**
Galgupha sp	1	0	0	0	0	0	**1**
Hymenoptera							
Andrenidae							
Andrena beameri[A]	0	0	0	0	1	0	**1**
Andrena carlini	0	0	0	1	0	0	**1**
Andrena commoda	0	0	0	0	2	0	**2**
Andrena cressonii	4	0	2	2	0	0	**8**
Andrena helianthiformis[A]	1	2	5	0	0	0	**8**
Andrena hippotes	1	0	0	0	0	0	**1**
Andrena macra	1	0	0	0	0	0	**1**
Andrena personata	1	0	1	1	0	1	**4**
Andrena platyparia[A]	1	0	0	0	0	0	**1**
Andrena rudbeckiae[A]	1	0	0	1	0	2	**4**
Andrena sp	0	3	0	3	0	1	**7**
Andrena ziziae[A]	0	0	2	0	0	0	**2**
Calliopsis andreniformis[A]	0	0	0	1	1	0	**2**
Protandrena bancrofti	0	0	0	4	1	1	**6**
Pseudopanurgus albitarsis	1	1	0	0	0	0	**2**
Apidae							
Anthophora abrupta	0	0	1	4	1	0	**6**
Anthophora bomboides	0	0	0	1	0	0	**1**
Anthophora walshii	0	0	0	0	1	0	**1**
Apis mellifera	34	33	21	285	55	26	**454**
Bombus auricomus	1	0	0	4	2	1	**8**
Bombus bimaculatus	0	6	1	17	45	16	**85**
Bombus fraternus	0	4	2	1	2	0	**9**
Bombus griseocollis	38	43	31	31	47	33	**223**
Bombus impatiens	0	0	0	0	2	1	**3**
Bombus pensylvanicus	4	2	4	5	3	5	**23**
Bombus sp	8	10	3	7	14	3	**45**
Bombus vagans	0	1	0	0	0	0	**1**

	Remnant			Reconstructed			
	2013	2014	2015	2013	2014	2015	**Total**
Ceratina sp (calcarata/ dupla/ miqmaki)	0	1	8	0	0	0	**9**
Ceratina strenua	0	4	2	0	0	0	**6**
Diadasia enavata	0	0	0	1	0	0	**1**
Eucera hamata	1	1	0	9	5	6	**22**
Melissodes comptoides	0	0	0	4	0	0	**4**
Melissodes coreopsis[A]	5	3	0	7	3	0	**18**
Melissodes sp	1	0	2	2	0	2	**7**
Nomada sp	0	0	0	2	0	0	**2**
Svastra obliqua[A]	6	0	1	10	0	1	**18**
Svastra sp	0	0	1	0	0	2	**3**
Triepeolus concavus[B]	1	0	0	0	0	0	**1**
Xylocopa virginica	18	3	3	5	2	7	**38**
Braconidae							
Cremnops haematodes	0	3	0	0	0	0	**3**
Cremnops sp	0	0	1	0	0	0	**1**
Schizoprymnus sp	0	0	0	1	0	0	**1**
Colletidae							
Colletes eulophi	3	0	0	1	0	0	**4**
Colletes latitarsis[A]	0	0	0	0	0	1	**1**
Colletes robertsonii[A]	1	0	1	1	3	1	**7**
Hylaeus sp (modestus/affinis/illinoisensis)	0	0	2	0	6	3	**11**
Crabronidae							
Astata unicolor	0	1	0	0	0	0	**1**
Cerceris sp	0	0	1	0	1	2	**4**
Formicidae							
Camponotus americanus	0	0	0	0	0	1	**1**
Crematogaster cerasi	1	0	0	0	0	0	**1**
Formica biophilica	4	5	0	0	13	0	**22**
Formica dolosa	0	0	1	0	0	7	**8**
Formica pallidefulva	0	0	17	0	0	0	**17**
Formica subsericea	5	2	25	0	0	5	**37**
Halictidae							
Agapostemon sp	0	0	2	0	0	0	**2**
Agapostemon texanus	0	0	3	2	0	3	**8**
Agapostemon virescens	0	0	6	2	1	1	**10**
Augochlora pura	0	0	0	0	1	0	**1**

	Remnant			Reconstructed			
	2013	2014	2015	2013	2014	2015	**Total**
Augochlorella aurata	27	40	103	14	12	48	**244**
Augochlorella persimilis	28	25	21	5	5	10	**94**
Augochlorella sp	0	0	7	2	2	23	**34**
Augochloropsis metallica	5	7	18	2	5	7	**44**
Halictus ligatus	3	6	26	4	12	30	**81**
Halictus parallelus	7	15	3	4	6	9	**44**
Halictus rubicundus	2	2	1	1	2	0	**8**
Lasioglossum (subgen. Dialictus)	10	51	18	45	51	21	**196**
Lasioglossum forbesii	0	0	0	0	0	1	**1**
Lasioglossum pectorale	0	0	0	1	0	1	**2**
Lasioglossum sp	0	0	0	1	0	0	**1**
Nomia nortoni	0	1	0	0	1	0	**2**
Sphecodes sp	1	0	0	0	0	1	**2**
Ichneumonidae							
Temelucha interruptor	0	0	0	0	1	0	**1**
Megachilidae							
Anthidiellum notatum	0	0	0	0	1	0	**1**
Coelioxys germana[B]	0	0	0	0	2	0	**2**
Coelioxys octodentata[B]	1	1	2	0	0	0	**4**
Coelioxys sayi[B]	0	1	0	1	0	0	**2**
Heriades carinata	5	0	1	2	1	0	**9**
Heriades variolosa/leavitti	0	7	0	0	0	1	**8**
Hoplitis pilosifrons	2	5	2	1	5	1	**16**
Hoplitis producta	0	8	5	1	0	1	**15**
Hoplitis spoliata	1	1	3	0	0	0	**5**
Megachile addenda[A]	0	1	0	0	2	1	**4**
Megachile brevis	12	13	7	3	5	0	**40**
Megachile exilis	3	1	0	0	0	1	**5**
Megachile frugalis	1	0	1	0	0	1	**3**
Megachile georgica	0	0	0	1	0	0	**1**
Megachile inimica[A]	0	0	0	1	0	0	**1**
Megachile mendica	1	2	8	0	3	2	**16**
Megachile montivaga	0	0	0	0	0	1	**1**
Megachile parallela[A]	0	0	1	2	2	0	**5**
Megachile petulans[A]	0	1	0	1	4	1	**7**
Megachile policaris	1	0	0	0	2	1	**4**
Megachile sp	0	2	2	3	0	2	**9**

	Remnant			Reconstructed			
	2013	2014	2015	2013	2014	2015	**Total**
Osmia conjuncta	2	0	0	0	0	0	**2**
Osmia cordata	1	0	0	3	0	0	**4**
Osmia georgica[A]	0	0	0	0	1	0	**1**
Osmia pumila	0	0	0	1	0	0	**1**
Osmia sp	0	0	2	0	0	1	**3**
Stelis lateralis[B]	0	0	1	0	1	0	**2**
Pompilidae							
Cryptocheilus hesperus	1	0	0	0	0	0	**1**
Entypus fulvicornis	1	0	0	0	0	0	**1**
Sphecidae							
Ammophila nigricans	0	0	0	0	4	0	**4**
Ammophila sp	1	0	0	2	0	1	**4**
Isodontia auripes	0	2	0	0	0	1	**3**
Prionyx atratus	1	0	0	0	0	0	**1**
Sceliphron caementarium	0	1	0	0	0	0	**1**
Sphex ichneumoneus	1	0	0	0	0	0	**1**
Sphex sp	0	1	0	0	0	0	**1**
Thynnidae							
Myzinum quinquecinctum	1	0	1	1	1	1	**5**
Vespidae							
Eurodynerus sp	0	2	0	0	1	0	**3**
Parancistrocerus fulvipes	0	0	3	0	0	0	**3**
Parancistrocerus leinotus	0	1	0	0	1	0	**2**
Parancistrocerus pedestris	0	0	2	0	0	0	**2**
Parancistrocerus pennsylvanicus	0	1	0	0	0	0	**1**
Parancistrocerus sp	0	4	0	0	1	0	**5**
Polistes fuscatus	4	5	2	1	4	1	**17**
Pterocheilus quinquefasciatus	0	0	1	0	0	0	**1**
Stenodynerus anormis	1	0	0	0	0	0	**1**
Stenodynerus fundatiformis	0	0	0	0	1	0	**1**
Stenodynerus sp	0	0	1	0	0	0	**1**
Lepidoptera							
Attevidae							
Atteva aurea	0	0	0	0	1	3	**4**
Hesperiidae							
Amblyscirtes nysa	2	0	0	0	1	0	**3**
Amblyscirtes vialis[C]	1	0	0	0	1	0	**2**

	Remnant			Reconstructed			
	2013	2014	2015	2013	2014	2015	**Total**
Anatrytone logan	0	0	2	1	2	1	**6**
Atalopedes campestris	8	0	0	8	0	1	**17**
Atrytone arogos[C]	0	1	0	0	1	0	**2**
Epargyreus clarus	0	0	1	0	1	5	**7**
Pholisora catullus	0	2	2	0	0	2	**6**
Poanes zabulon	0	1	0	0	0	0	**1**
Polites origenes[C]	0	4	2	6	0	2	**14**
Polites themistocles	9	8	21	5	2	4	**49**
Problema byssus[C]	1	2	0	0	5	0	**8**
Pyrgus communis	0	1	0	0	0	0	**1**
Thorybes bathyllus[C]	1	1	1	0	0	0	**3**
Thorybes pylades[C]	0	0	2	0	0	1	**3**
Lycaenidae							
Cupido comyntas	38	30	5	87	37	13	**210**
Lycaena dione	0	0	0	1	0	1	**2**
Satyrium titus	1	2	0	0	0	0	**3**
Strymon melinus	1	0	1	0	0	2	**4**
Nymphalidae							
Agraulis vanillae	0	0	1	0	0	0	**1**
Asterocampa celtis	0	32	0	0	0	4	**36**
Chlosyne nycteis[C]	0	1	0	1	2	1	**5**
Danaus plexippus	3	3	3	1	1	1	**12**
Euptoieta claudia	7	2	1	0	0	1	**11**
Junonia coenia	0	0	1	1	0	0	**2**
Phyciodes tharos	21	10	1	34	11	9	**86**
Speyeria cybele	6	65	12	6	9	6	**104**
Speyeria idalia[C]	8	1	7	2	1	1	**20**
Vanessa atalanta	0	0	0	0	0	2	**2**
Vanessa cardui	0	0	0	0	0	1	**1**
Vanessa sp	2	0	0	1	0	7	**10**
Vanessa virginiensis	0	1	1	2	2	0	**6**
Papilionidae							
Papilio cresphontes	0	0	2	0	0	0	**2**
Papilio glaucus	0	1	0	1	0	1	**3**
Papilio polyxenes	1	0	0	0	0	0	**1**
Papilio sp	0	0	0	1	0	0	**1**
Protographium marcellus[C]	1	1	0	1	0	0	**3**
Pieridae							

	Remnant			Reconstructed			
	2013	2014	2015	2013	2014	2015	**Total**
Colias philodice/eurytheme	18	9	5	13	3	5	**53**
Pieris rapae	15	12	3	4	13	0	**47**
Scythrididae							
Scythris eboracensis	64	6	0	0	3	2	**75**
Scythris trivinctella	1	0	0	0	0	0	**1**
Sphingidae							
Hemaris diffinis	3	0	0	1	0	0	**4**
Hemaris sp	4	1	0	1	1	1	**8**
Tortricidae							
Grapholita interstinctana	0	0	0	0	0	1	**1**
Neuroptera							
Chrysopidae	0	1	0	0	0	0	**1**
Chrysopa sp	0	1	0	0	0	0	**1**
Orthoptera							
Tettigoniidae	1	0	1	0	0	0	**2**
Scudderia sp	1	0	0	0	0	0	**1**

Table S1.3. Forb abundance ANOVA table. Fixed effects are displayed from a generalized linear mixed model (Poisson error distribution: log link) assessing the effects of site type, study year, and the site type x study year interaction on forb abundance across ten Kansas tallgrass prairies. Abundance values were rarefied to nine total samples. *P*-values were fit via parametric bootstrapping of the likelihood ratio test statistic. *P*-values from a chi-square distribution are provided for reference.

Factor	χ^2	D.f.	*P (chi-sq.)*	*P (bootstrap)*
Site Type	4.68	1	0.030	0.064
Year	9.57	2	0.008	0.011
Site Type x Year	9.71	2	0.008	0.023

Table S1.4. Forb diversity ANOVA table. Fixed effects are displayed from a general linear mixed model assessing the effects of site type, study year, and the site type x study year interaction on forb diversity across ten Kansas tallgrass prairies.

Factor	Num D.f.	Den D.f.	*F*	*P*
Intercept	1	16	96.52	< 0.0001
Site Type	1	8	8.08	0.022
Year	2	16	1.55	0.242
Site Type x Year	2	16	0.67	0.528

Table S1.5. PERMANOVA examining the effects of site type, study year, and their interaction on forb community composition. Bray-Curtis dissimilarity was used (999 permutations).

Between-Subjects (Site) Effects					
	D.f.	S.S.	M.S.	*pseudo-F*	*P*
site type	1	3755.7	3755.7	1.50	0.014
residuals	8	20065	2508.1		
Within-Subjects (Site) Effects					
	D.f.	S.S.	M.S.	*pseudo-F*	*P*
study year	2	6402.4	3201.2	1.66	0.031
site type x study year	2	2737.9	1368.9	0.71	0.854
residuals	16	30844	1927.8		

Table S1.6. Significant forb indicator species of prairie remnants and reconstructed prairies, based on Indicator Species Analysis. CoC = Coefficient of Conservatism for Kansas Vascular Plants (Freeman 2012). † = only recorded at reconstructed prairies. ‡ = only recorded at remnant sites. NN = non-native species. CoC values were not recorded for *H. helianthoides* or *D. carolinianum* because two subspecies with differing CoC values occur for each of these species in Kansas, and we did not identify forbs to subspecies. CoC values do not apply to non-native species.

Species (Family)	Site Type	*P*	CoC
Rudbeckia hirta (Asteraceae)	reconstructed	0.028	2
Monarda fistulosa† (Lamiaceae)	reconstructed	0.002	3
Heliopsis helianthoides† (Asteraceae)	reconstructed	0.012	--
Chamaecrista fasciculata† (Fabaceae)	reconstructed	0.017	2
Penstemon digitalis† (Plantaginaceae)	reconstructed	0.019	4
Triodanis perfoliata† (Campanulaceae)	reconstructed	0.044	2
Psoralidium tenuiflorum‡ (Fabaceae)	remnant	0.001	3
Lobelia spicata (Campanulaceae)	remnant	0.001	6
Asclepias tuberosa (Asclepiadaceae)	remnant	0.008	6
Sisyrinchium campestre‡ (Iridaceae)	remnant	0.003	6
Potentilla recta (Rosaceae)	remnant	0.021	NN
Apocynum cannabinum (Apocynaceae)	remnant	0.046	0
Hypoxis hirsuta‡ (Liliaceae)	remnant	0.006	5
Rosa sp.‡ (Rosaceae)	remnant	0.005	--
Ruellia humilis‡ (Acanthaceae)	remnant	0.004	3
Euphorbia corollata (Euphorbiaceae)	remnant	0.009	5
Phlox pilosa (Polemoniaceae)	remnant	0.005	7
Comandra umbellata‡ (Santalaceae)	remnant	0.014	6
Leucanthemum vulgare‡ (Asteraceae)	remnant	0.014	NN
Zizia aurea‡ (Apiaceae)	remnant	0.014	5
Delphinium carolinianum‡ (Ranunculaceae)	remnant	0.043	--
Oenothera speciosa‡ (Onagraceae)	remnant	0.041	2
Tradescantia bracteata‡ (Commelinaceae)	remnant	0.037	5

Table S1.7. ANOVA tables for flower visitor, bee, and beetle diversity. Fixed effects are displayed from three separate general linear mixed models assessing the effects of site type, study year, and the site type x study year interaction on flower visitor (top), bee (middle), and phytophagous beetle (bottom) diversity across ten Kansas tallgrass prairies.

All Flower Visiting Insects				
Factor	**Num D.f.**	**Den D.f.**	***F***	***P***
Intercept	1	16	200.11	< 0.0001
Site Type	1	8	0.05	0.819
Year	2	16	2.74	0.095
Site Type x Year	2	16	2.67	0.100
Bees				
Intercept	1	16	132.66	< 0.0001
Site Type	1	8	0.57	0.472
Year	2	16	1.61	0.230
Site Type x Year	2	16	2.47	0.116
Phytophagous Beetles				
Intercept	1	16	186.96	< 0.0001
Site Type	1	8	0.22	0.655
Year	2	16	0.81	0.461
Site Type x Year	2	16	0.38	0.690

Table S1.8: ANOVA tables for flower visitor, bee, and beetle abundance. Fixed effects are displayed from three generalized linear mixed models (Poisson error distribution: log link) assessing the effects of site type, study year, and the site type x study year interaction on the abundance of flower visitors, bees, and phytophagous beetles, respectively, across ten Kansas tallgrass prairies. Abundance values were rarefied to nine total samples. *P*-values were fit via parametric bootstrapping of the likelihood ratio test statistic. *P*-values from a chi-square distribution are provided for reference.

All Flower Visiting Insects				
Factor	χ^2	**D.f.**	***P (chi-sq)***	***P (bootstrap)***
Site Type	0.23	1	0.633	0.682
Year	0.50	2	0.778	0.819
Site Type x Year	3.70	2	0.158	0.228
Bees				
Site Type	0.25	1	0.616	0.680
Year	0.73	2	0.695	0.770
Site Type x Year	3.00	2	0.223	0.324
Phytophagous Beetles				
Site Type	1.54	1	0.214	0.254
Year	8.72	2	0.013	0.026
Site Type x Year	5.85	2	0.054	0.107

Table S1.9. PERMANOVA table examining the effects of site type, study year, and their interaction on bee community composition. Bray-Curtis dissimilarity was used (999 permutations).

Between Subjects (Site) Effects					
	D.f.	S.S.	M.S.	*F*	*P*
site type	1	2129.7	2129.7	1.85	0.061
residuals	8	9186	1148.3		
Within Subjects (Site) Effects					
	D.f.	S.S.	M.S.	*F*	*P*
study year	2	9247	4623.5	3.51	0.002
site type x study year	2	3439.8	1719.9	1.31	0.178
residuals	16	21072	1317		

Table S1.10. PERMANOVA table examining the effects of site type, study year, and their interaction on flower visitor community composition. Bray-Curtis dissimilarity was used (999 permutations).

Between Subjects (Site) Effects					
	D.f.	S.S.	M.S.	*pseudo-F*	*P*
site type	1	1383.1	1383.1	0.96	0.554
residuals	8	11572	1446.5		
Within Subjects (Site) Effects					
	D.f.	S.S.	M.S.	*pseudo-F*	*P*
study year	2	11523	5761.5	3.46	0.001
site type x study year	2	3321.2	1660.6	1.00	0.473
residuals	16	26657	1666		

Table S1.11. PERMANOVA table examining the effects of site type, study year, and the site type x study year interaction on phytophagous beetle community composition. Bray-Curtis dissimilarity was used (999 permutations).

Between Subjects (Site) Effects					
	D.f.	S.S.	M.S.	*pseudo-F*	*P*
site type	1	1069	1069	0.71	0.620
residuals	8	11973	1496.6		
Within Subjects (Site) Effects					
	D.f.	S.S.	M.S.	*pseudo-F*	*P*
study year	2	5769.5	2884.7	2.29	0.032
site type x study year	2	3494.5	1747.3	1.39	0.199
residuals	16	20172	1260.7		

Table S1.12. Significant indicators of each study year for flower visiting insects, bees, and phytophagous beetles. *P*-values are based on Indicator Species Analysis. NS = non-significant.

Species	Year	$P_{all\ visitors}$	$P_{bees\ only}$	$P_{phyto.\ beetles\ only}$
Atalopedes campestris	2013	0.002	--	--
Svastra obliqua	2013	0.003	0.001	--
Colias philodice/eurytheme	2013	0.024	--	--
Odontocorynus salebrosus	2013	0.027	--	0.031
Melissodes coreopsis	2013	0.034	0.015	--
Geron sp.	2013	0.042	--	--
Apiomerus sp. (likely cazieri)	2013	0.027	--	--
Bombus sp.	2014	0.019	0.036	--
Bombus bimaculatus	2014	0.035	> 0.05 (NS)	--
Bombus fraternus	2014	> 0.05 (NS)	0.024	--
Lygaeus kalmii	2014	0.007	--	--
Toxomerus marginatus	2015	0.013	--	--
Halictus ligatus	2015	0.013	0.011	--
Augochlorella aurata	2015	0.005	0.032	--
Augochlorella sp.	2015	0.015	0.013	--
Sphaerophoria contigua	2015	0.014	--	--
Eristalis transversa	2015	0.009	--	--
Megachile mendica	2015	0.043	> 0.05 (NS)	--
Epargyreus clarus	2015	0.012	--	--
Agapostemon texanus	2015	0.038	0.017	--

Appendix 2: Supplemental Figures and Tables for Chapter 2

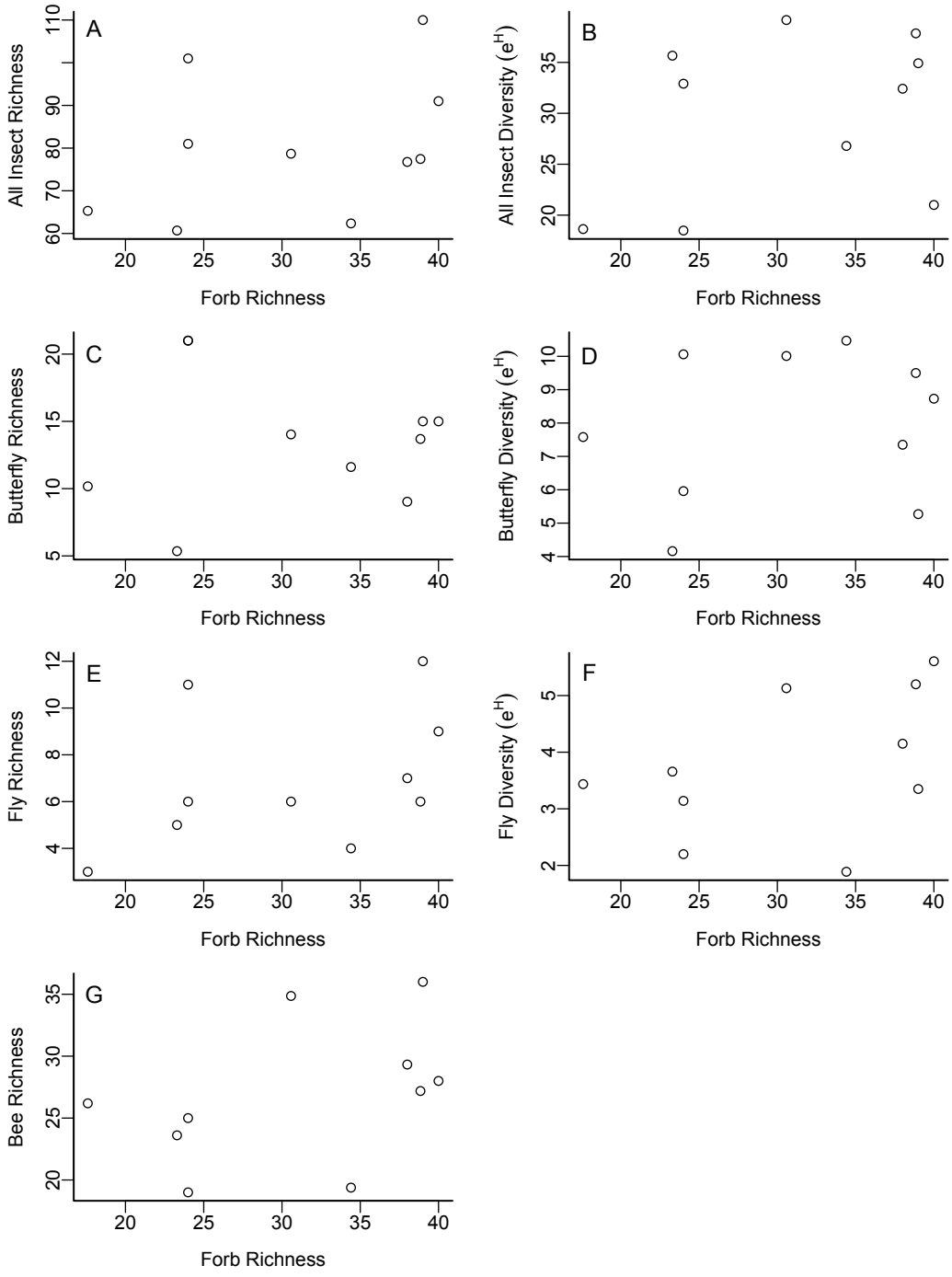

Figure S2.1. Scatterplots of the relationship between forb richness across ten Kansas tallgrass prairies and the rarefied richness and diversity of **A-B)** all flower visiting insects; **C-D)** butterflies; **E-F)** syrphid and bombyliid flies; **G)** bee richness. All richness values were rarefied to nine total surveys to account for differences in sampling effort. All relationships were non-significant based on correlation tests. The significant relationship between forb richness and bee diversity is displayed in Fig. 2.

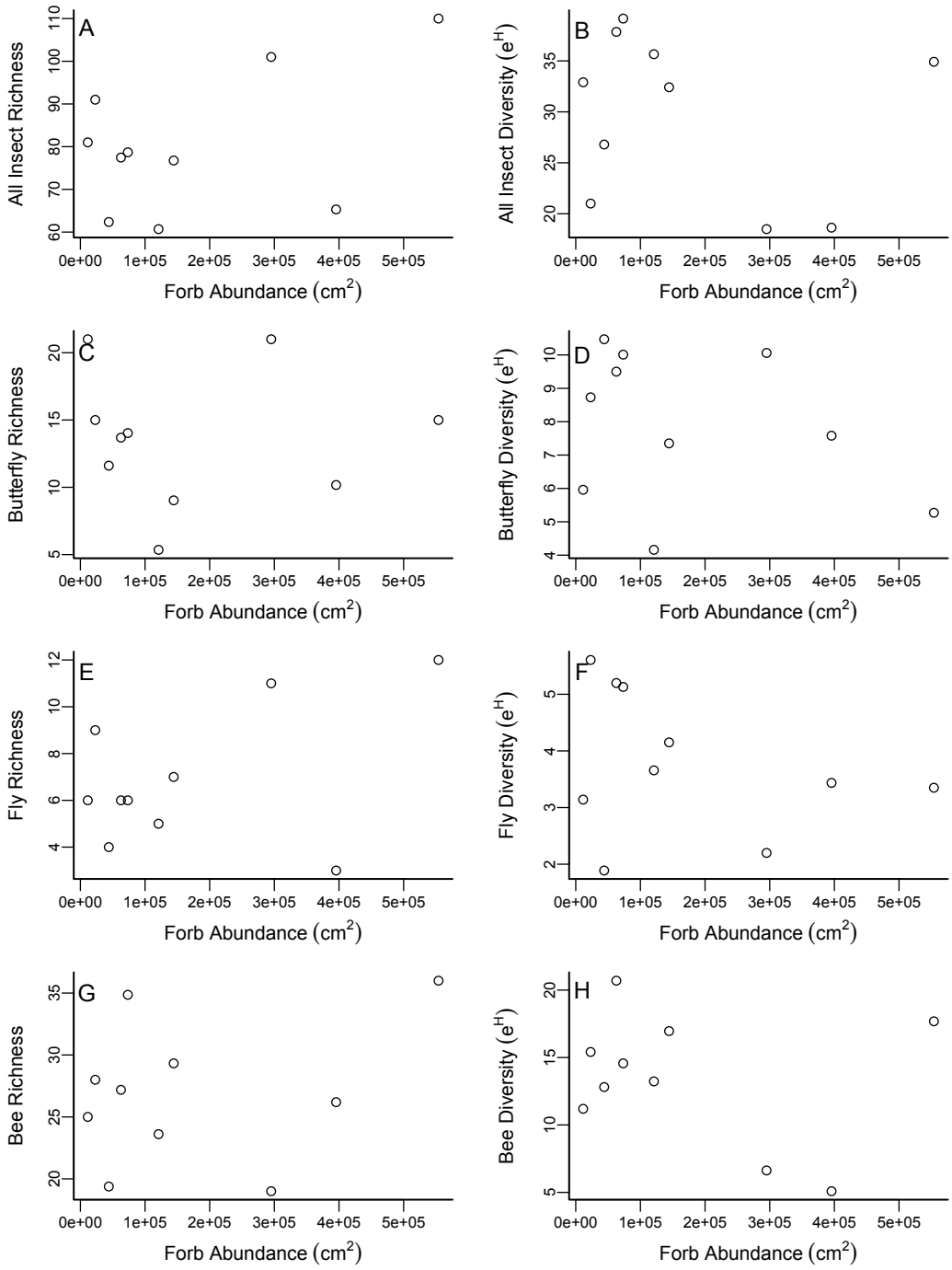

Figure S2.2. Scatterplots of the relationships between rarefied forb abundance across ten Kansas tallgrass prairies and the rarefied richness and diversity of **A-B)** all flower visiting insects; **C-D)** butterflies; **E-F)** Syrphid and bombyliid flies; **G-H)** bees. Forb abundance was measured as the size of the floral display in cm^2 and was rarefied to nine total surveys to account for differences in sampling effort. All relationships were non-significant based on correlation tests.

Table S2.1. The fifteen most frequently-recorded forb-flower visitor interactions, summed across all tallgrass prairie study sites and years. A total of 6679 interactions were recorded, encompassing 1359 unique combinations of forb and flower visitor species.

Rank	Interaction (Insect, Forb)	Number Recorded	Cumulative Number Insects Involved in Interactions	Cumulative % of All Interactions
1	*Toxomerus marginatus, Erigeron strigosus*	358	358	5.36%
2	*Apis mellifera, Melilotus officinalis*	234	592	8.86%
3	*Typocerus octonotatus, Rudbeckia hirta*	152	744	11.14%
4	*Cryptorhopalum triste, Achillea millefolium*	138	882	13.21%
5	*Diabrotica cristata Amorpha canescens*	120	1002	15.00%
6	*Typocerus sp, Rudbeckia hirta*	117	1119	16.75%
7	*Diabrotica cristata, Rudbeckia hirta*	110	1229	18.40%
8	*Typocerus octonotatus, Ratibida pinnata*	110	1339	20.05%
9	*Apis mellifera, Penstemon digitalis*	91	1430	21.41%
10	*Diabrotica cristata, Daucus carota*	89	1519	22.74%
11	*Speyeria cybele, Asclepias tuberosa*	87	1606	24.05%
12	*Diabrotica cristata, Trifolium pratense*	86	1692	25.33%
13	*Cryptorhopalum triste, Erigeron strigosus*	83	1775	26.58%
14	*Diabrotica cristata, Ceanothus americanus*	73	1848	27.67%
15	*Chauliognathus marginatus, Melilotus alba*	71	1919	28.73%

Appendix 3: Supplemental Figures and Tables for Chapter 3

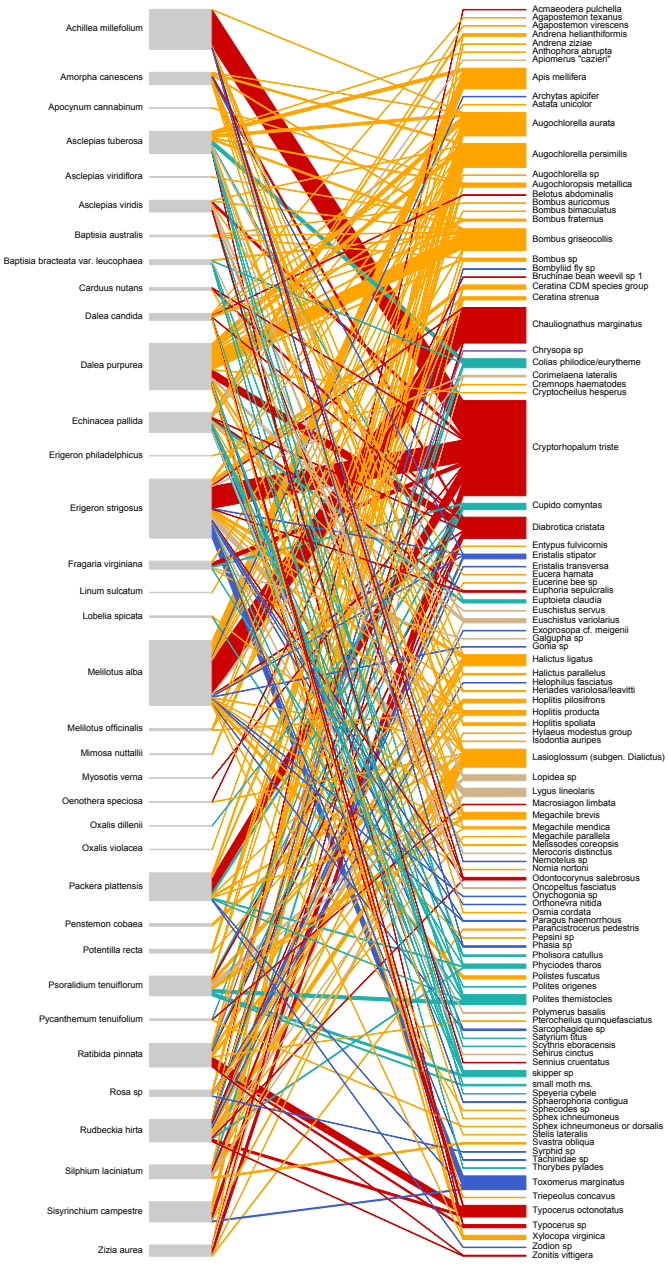

Figure S3.1. Network of interactions between forbs (grey boxes) and flower visiting insects (colored boxes) recorded at Anderson Family prairie remnant from 2013-2015. Box width is proportional to the number of interactions involving a given species. Insect boxes are colored by Order (Coleoptera = red, Diptera = dark blue, Hemiptera = tan, Hymenoptera = orange, Lepidoptera = light blue, Other = purple).

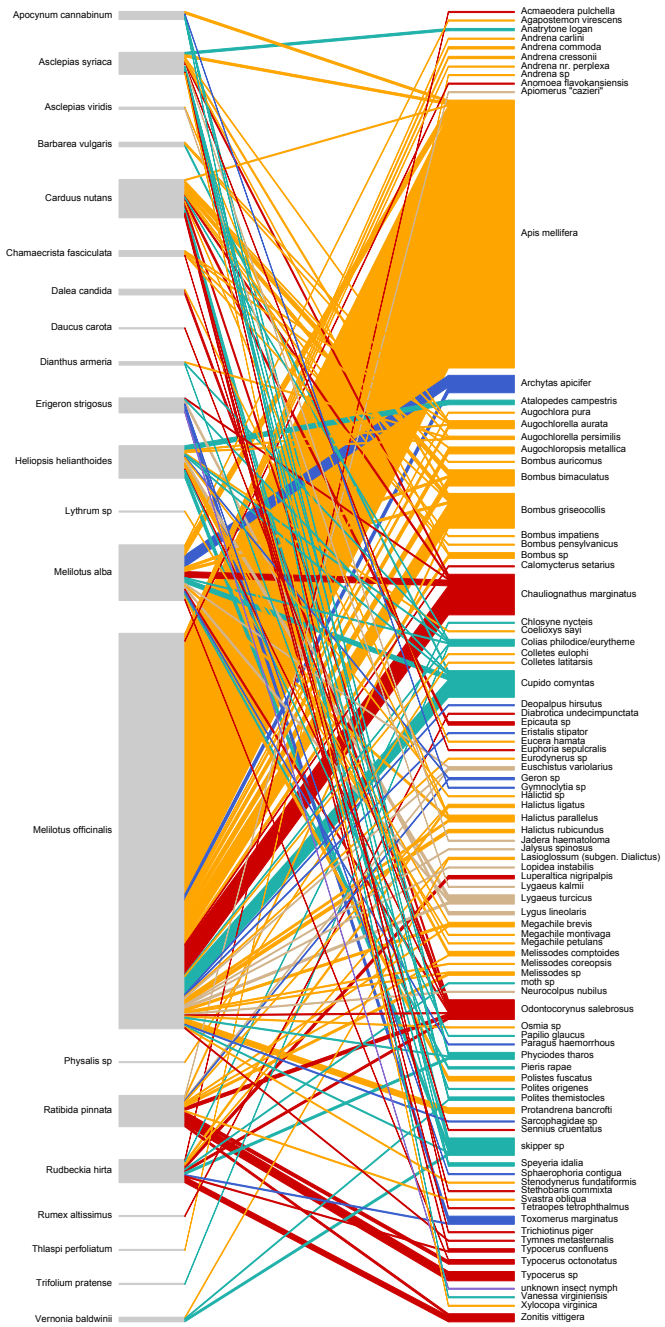

Figure S3.2. Network of interactions between forbs (grey boxes) and flower visiting insects (colored boxes) recorded at Baker Farm reconstructed prairie from 2013-2015. Box width is proportional to the number of interactions involving a given species. Insect boxes are colored by Order (Coleoptera = red, Diptera = dark blue, Hemiptera = tan, Hymenoptera = orange, Lepidoptera = light blue, Other = purple).

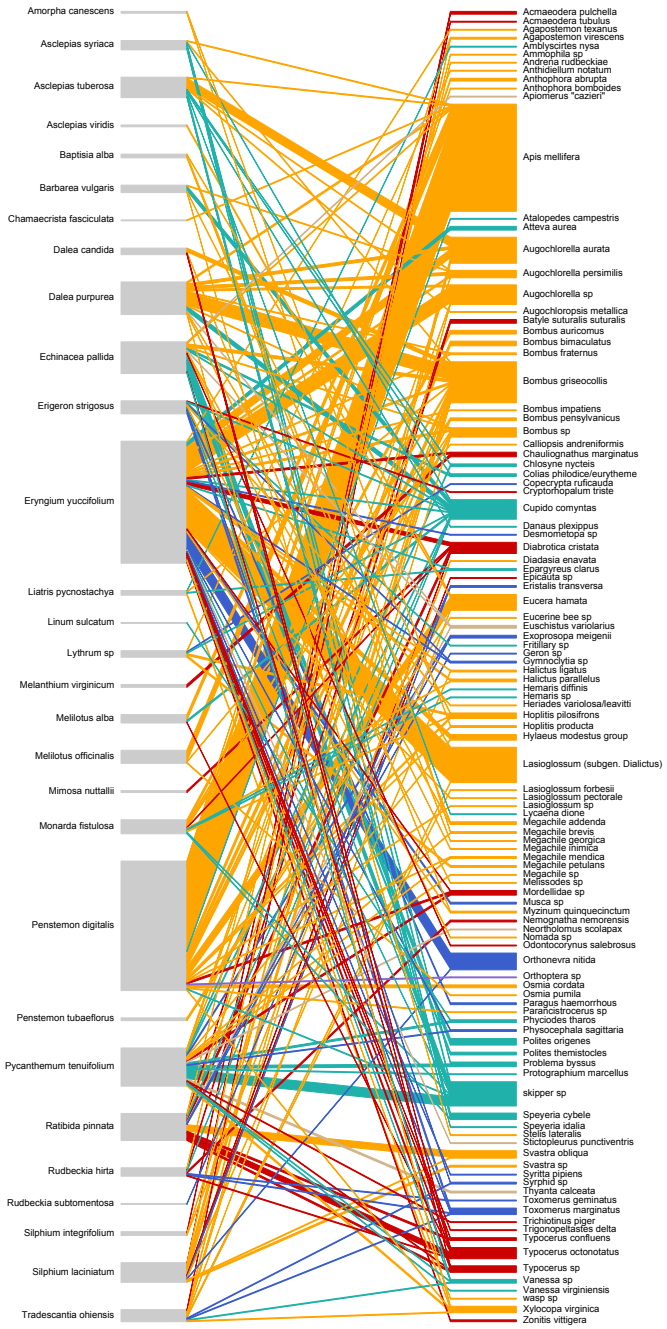

Figure S3.3. Network of interactions between forbs (grey boxes) and flower visiting insects (colored boxes) recorded at Busby reconstructed prairie from 2013-2015. Box width is proportional to the number of interactions involving a given species. Insect boxes are colored by Order (Coleoptera = red, Diptera = dark blue, Hemiptera = tan, Hymenoptera = orange, Lepidoptera = light blue, Other = purple).

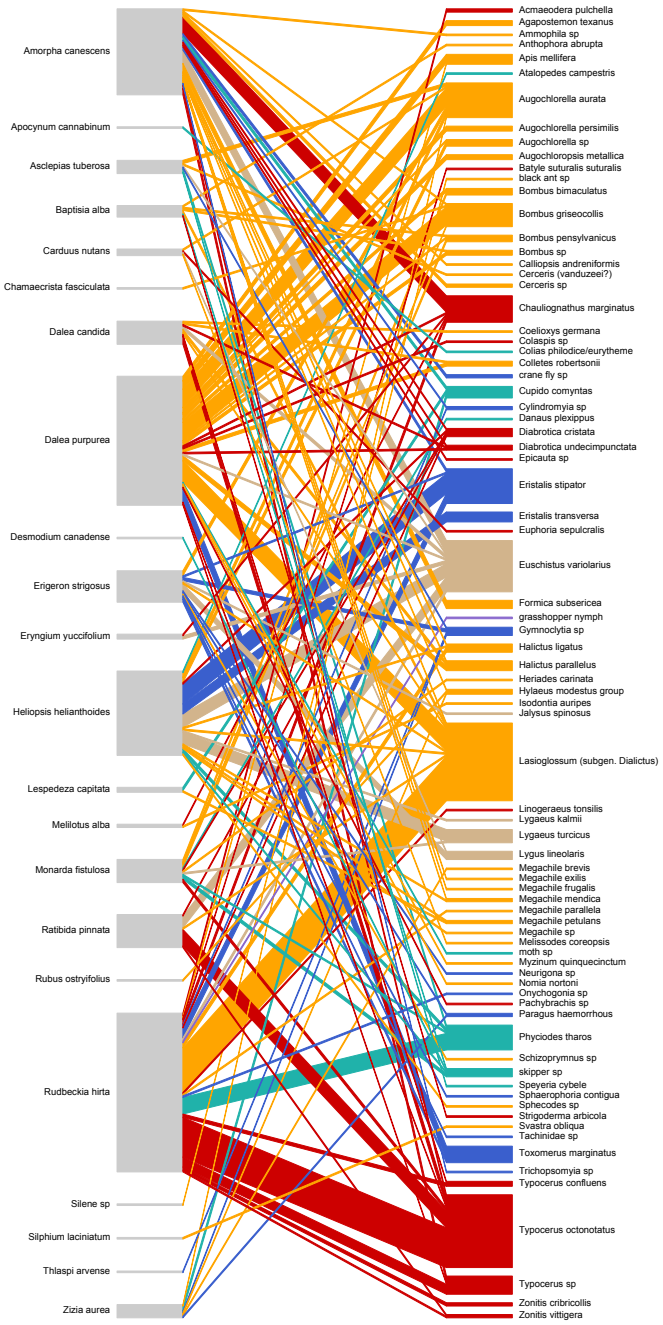

Figure S3.4. Network of interactions between forbs (grey boxes) and flower visiting insects (colored boxes) recorded at Byers Family reconstructed prairie from 2013-2015. Box width is proportional to the number of interactions involving a given species. Insect boxes are colored by Order (Coleoptera = red, Diptera = dark blue, Hemiptera = tan, Hymenoptera = orange, Lepidoptera = light blue, Other = purple).

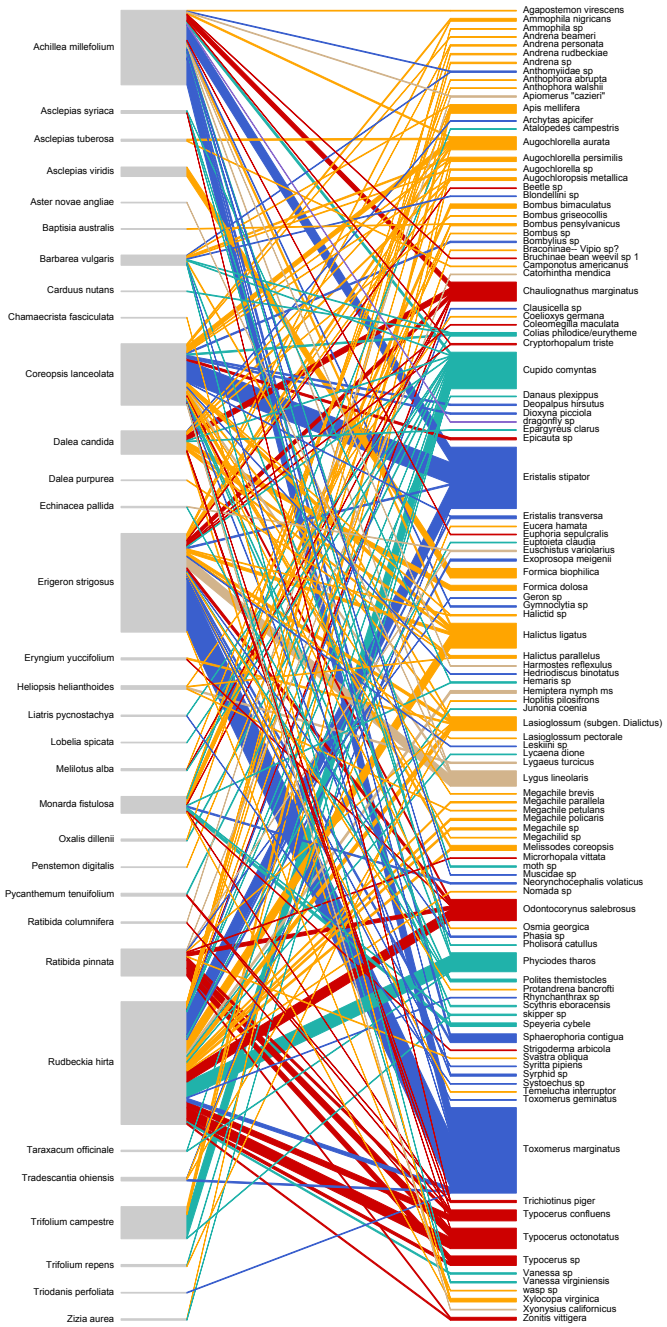

Figure S3.5. Network of interactions between forbs (grey boxes) and flower visiting insects (colored boxes) recorded at Coombs reconstructed prairie from 2013-2015. Box width is proportional to the number of interactions involving a given species. Insect boxes are colored by Order (Coleoptera = red, Diptera = dark blue, Hemiptera = tan, Hymenoptera = orange, Lepidoptera = light blue, Other = purple).

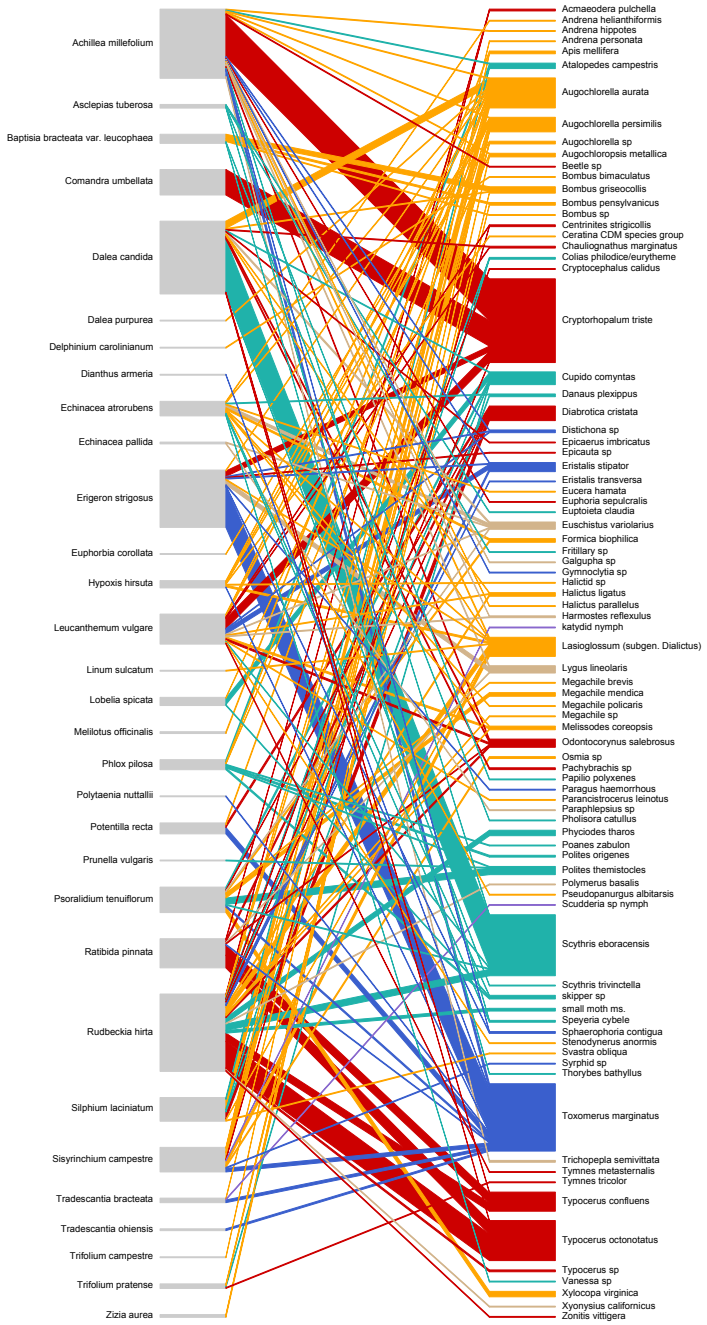

Figure S3.6. Network of interactions between forbs (grey boxes) and flower visiting insects (colored boxes) recorded at Guess prairie remnant from 2013-2015. Box width is proportional to the number of interactions involving a given species. Insect boxes are colored by Order (Coleoptera = red, Diptera = dark blue, Hemiptera = tan, Hymenoptera = orange, Lepidoptera = light blue, Other = purple).

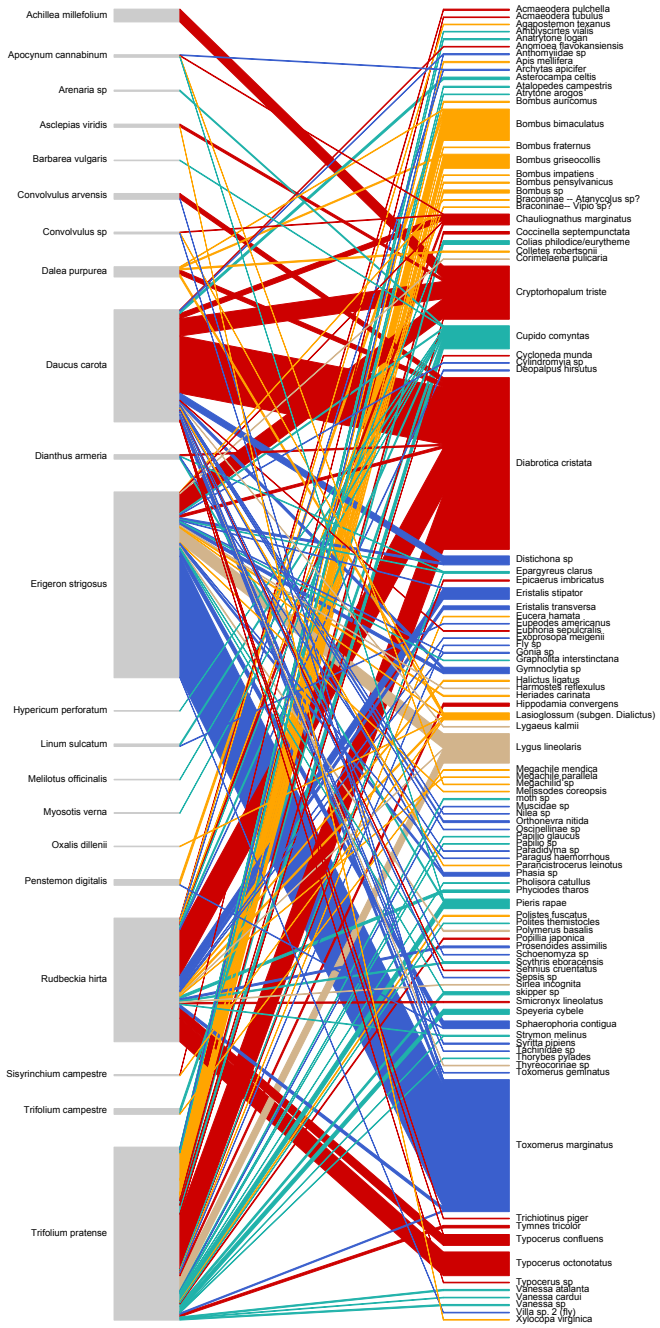

Figure S3.7. Network of interactions between forbs (grey boxes) and flower visiting insects (colored boxes) recorded at Kettle-Look reconstructed prairie from 2013-2015. Box width is proportional to the number of interactions involving a given species. Insect boxes are colored by Order (Coleoptera = red, Diptera = dark blue, Hemiptera = tan, Hymenoptera = orange, Lepidoptera = light blue, Other = purple).

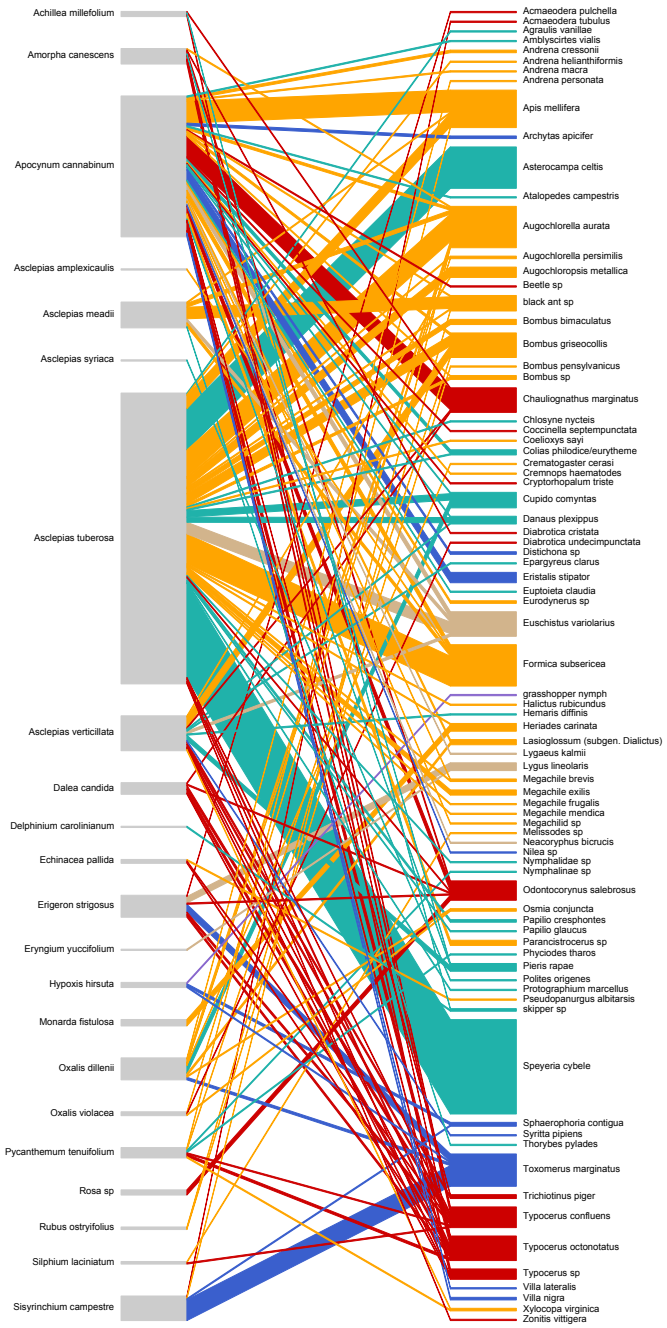

Figure S3.8. Network of interactions between forbs (grey boxes) and flower visiting insects (colored boxes) recorded at Rockefeller prairie remnant from 2013-2015. Box width is proportional to the number of interactions involving a given species. Insect boxes are colored by Order (Coleoptera = red, Diptera = dark blue, Hemiptera = tan, Hymenoptera = orange, Lepidoptera = light blue, Other = purple).

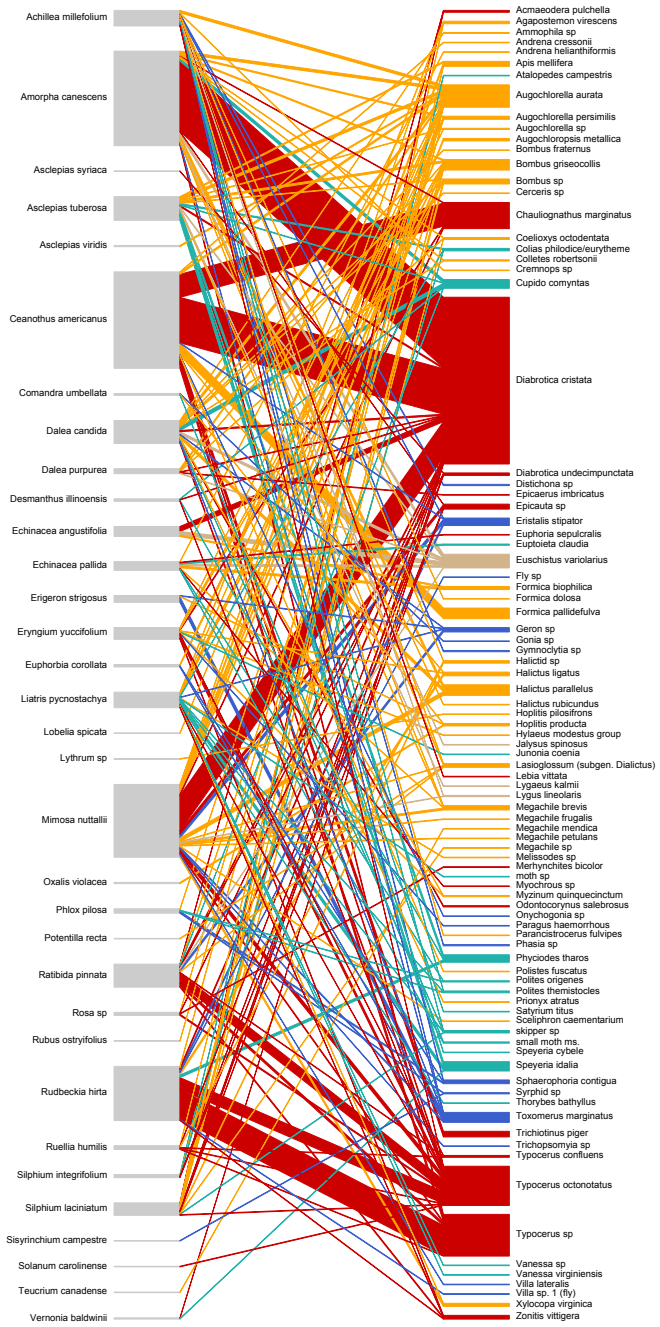

Figure S3.9. Network of interactions between forbs (grey boxes) and flower visiting insects (colored boxes) recorded at Snyder prairie remnant from 2013-2015. Box width is proportional to the number of interactions involving a given species. Insect boxes are colored by Order (Coleoptera = red, Diptera = dark blue, Hemiptera = tan, Hymenoptera = orange, Lepidoptera = light blue, Other = purple).

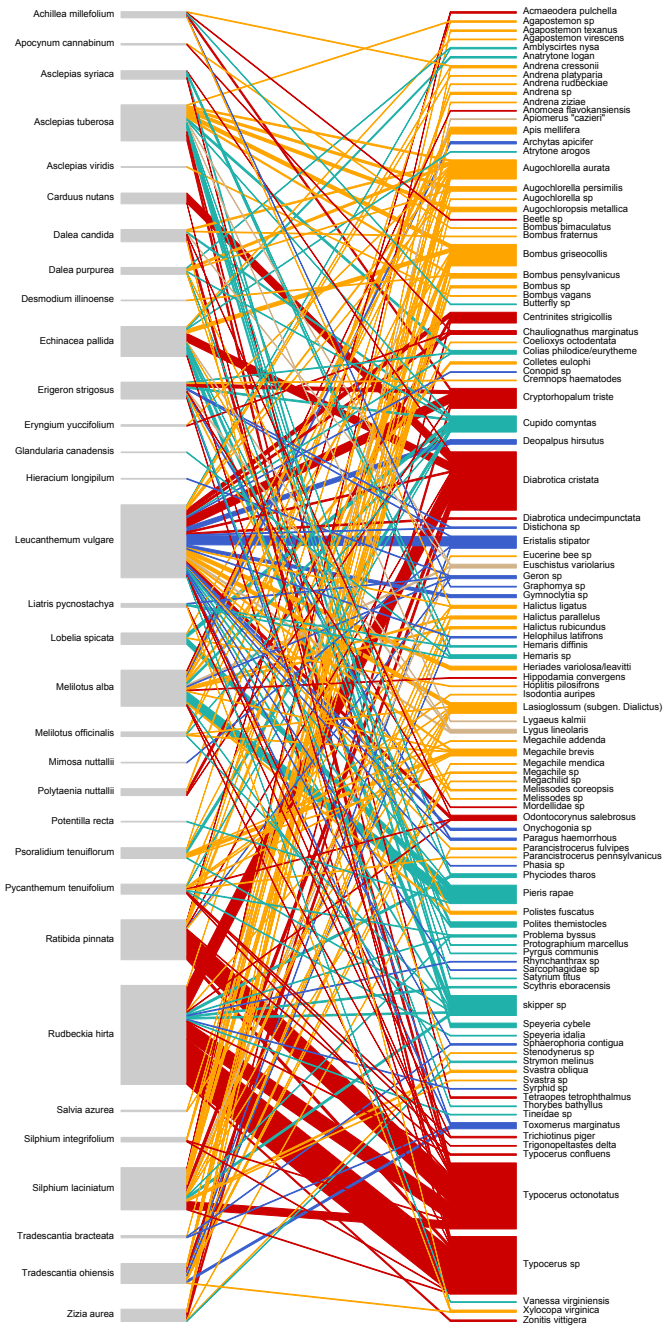

Figure S3.10. Network of interactions between forbs (grey boxes) and flower visiting insects (colored boxes) recorded at Teal Lake prairie remnant from 2013-2015. Box width is proportional to the number of interactions involving a given species. Insect boxes are colored by Order (Coleoptera = red, Diptera = dark blue, Hemiptera = tan, Hymenoptera = orange, Lepidoptera = light blue, Other = purple).

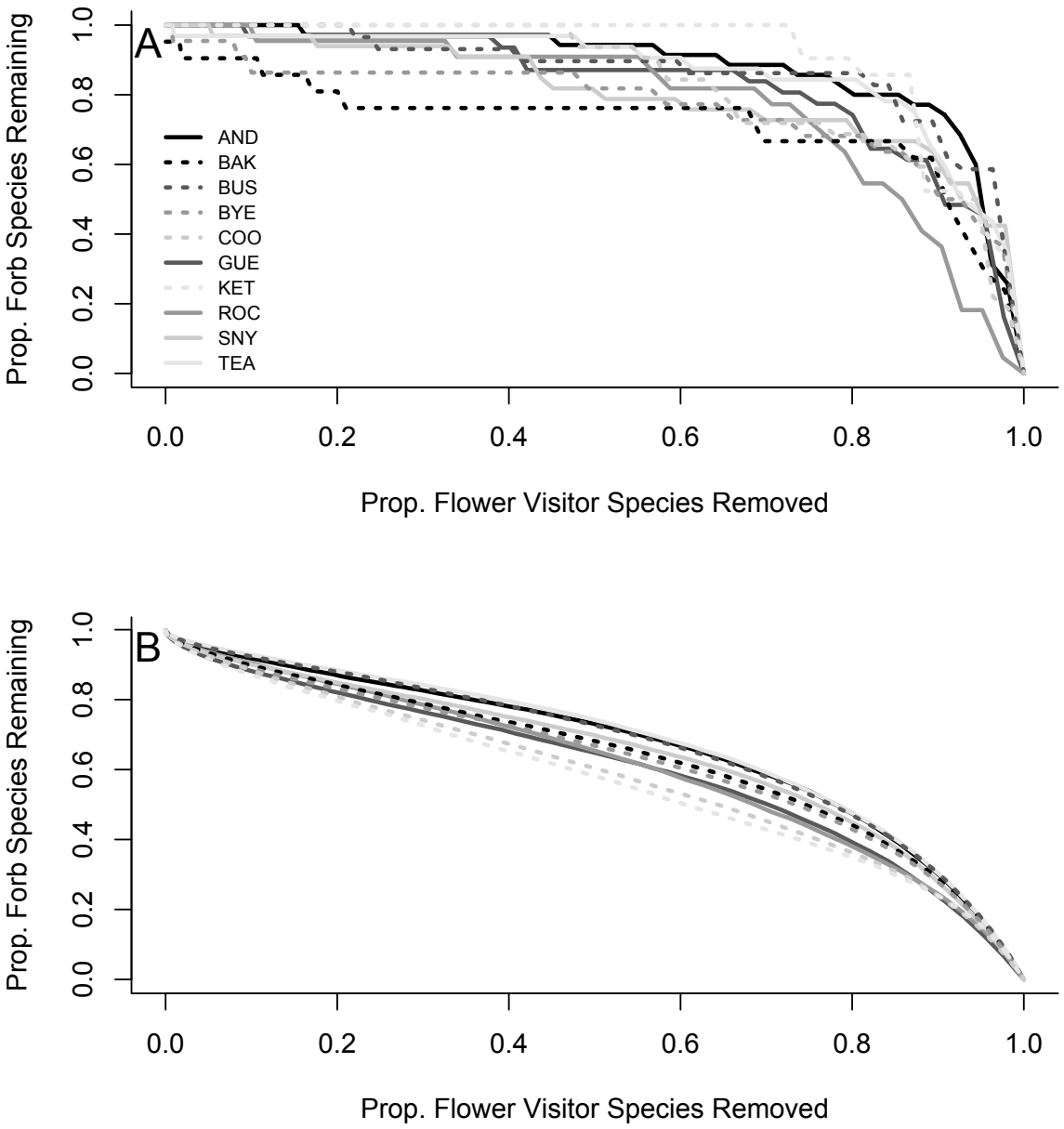

Figure S3.11. Plots of species removal simulations, where flower visitors were removed **A)** deterministically, from the least abundant to most abundant species, and **B)** randomly, with values averaged across 1000 replicate simulations. Solid lines signify remnant prairies, and dashed lines signify prairies reconstructed on former croplands.